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# THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST[1]

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ONE method of ascertaining the height of a mountain is with a single instrument, the barometer; another method is by triangulation with several instruments. Thus we may differ from Johannsen in his remark that morphology as a science of great collections in museums is of no value in genetics. The brilliant progress in heredity of the last nine years, beginning in 1903 with the rediscovery of Mendel's law, should not blind us to the four broad inductions from paleontology,[2] that transformation is a matter of thousands or hundreds of thousands of years, that to the living observer all living things may be delusively stationary, that invisible tides of genetic change may be setting in one direction or another observable only over very long periods of time,

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[2] Osborn, Henry F., "Darwin and Palæontology." One of the addresses in "Fifty Years of Darwinism." 8vo. Henry Holt & Co., New York, May 1, 1909.

that discontinuous mutations or saltations may be mere ripples on the surface of these tides.

Whatever the truth as to this thought, by a strange paradox it is certain that some stationary characters, some apparently dead things in the eyes of the zoologist and botanist, become movable and alive in the eyes of the paleontologist. Thus a paleontologist comes before the Harvey Society of Physiologists and Physicians with the conviction that his vision is of a different angle from that of the experimentalist, and that by the triangulation of experiment, of anatomy and of paleontology the truth may at least be more nearly approached.

Is there more evidence of discontinuity and of lawlessness, or of continuity and of law, in the origin of new characters? Perhaps no more appropriate question could be chosen as the subject of a lecture in memory of William Harvey, the author of the doctrine of epigenesis, for the essence of this doctrine is that of "successive differentiation of a relatively homogeneous rudiment into the parts and structures which are characteristic of the adult." Paleontology is at one with embryology in the belief that differentiation is in the main gradual and continuous.

Yet to our question the answer prevailing among experimentalists and Mendelians at the present time is that there is little evidence either for continuity or for law; this despite the fact that a large part of the evidence for discontinuity in the origin of characters is most unsound. In fact, our first purpose in this Harvey Lecture is to show how surprisingly unsound this evidence is when we consider that discontinuity has become practically a dogma among a very large number of zoologists and botanists. It is true that the evidence for discontinuity in the *heredity* of characters is as convincing as that for discontinuity in the *genesis* of characters is debatable. Our second purpose in this Harvey Lecture is to show that the evidence for continuity in the genesis of certain characters in man and other mammals is very

strong indeed, further, that some of these characters, while apparently continuous in origin, certainly become discontinuous in heredity; from which it follows that discontinuity in heredity constitutes no proof of discontinuity in origin.

The question is, how do these manifold characters of which the body is made up arise, continuously or discontinuously? A conservative opinion from what may be gathered in the whole field of observation at the present time is that while the greater part of evolution is continuous, especially in the origins of certain parts and in the development of certain proportions, there must also be a discontinuity, especially in numerical or meristic structures, such as vertebræ and teeth, and in chemical components and reactions which are essentially antithetic or discontinuous. In other words, there is both continuity and discontinuity, and one problem is to show what is continuous and what is discontinuous.

The history of "characters" is our quest, and now that attention is concentrated all along the line of observation in plants and animals, living and fossil, on the genesis and behavior of single characters, we have laid the train for substantial progress. A vast gain is that which relegates the problem of species to a side issue, or rather to an incidental result of the accumulation of a greater or less number of units.

A "character" may be racial shape of head or length of limb, it may be a cusplet on a grinding tooth, color of hair, or a sportive white lock of hair, it may be the brown or blue color of the eye, it may be the speed of a horse, or the obstinacy of a mule, in short, any structure or function, simple or extremely complex, which is stable and distinct in heredity. A "new character" is something which is unknown before, it may be a new unit, like the horns of cattle, it may be a new form or proportion of such a unit. "I understand by the term unit character," observes Morgan, "any particular structure or function that may appear in heredity independent of

other characters. Such unit characters may in themselves be extremely complex and include the possibility of further splitting up." The point where Mendelism bears on the problem is, therefore, the continuous or discontinuous origin of the thousands of characters which display this more or less complete discontinuity in heredity.

## I. EVIDENCES FOR DISCONTINUITY

Darwin has been widely misunderstood of late as believing in continuity,[3] whereas he chiefly believed in discontinuity.[4] In his original (1859) and final (1872) opinion evolution is due chiefly to the selection of heritable "individual differences"; these have been understood by some as "fluctuations." His true meaning as to these *individual differences* is to be found in the cases he cited, which may be collected from hundreds of observations in the "Origin of Species" and "Variation of Animals and Plants under Domestication," to the effect that such individual differences or *new characters* were in the nature of *minor saltations,* structural or functional, and always hereditary. If we note some of the observations which he assembled in commenting on the genesis of the race horse and the grayhound, breeds which he used by way of illustration of the genesis of new forms in nature, we find they include such suddenly appearing new characters as horn rudiments, taillessness, curliness of the hair, characters which are discontinuous in Bateson's sense, or mutations in that of De Vries;[5] intermingled with these new characters he cited

[3] Cf. Poulton, E. B., "Darwin and the 'Origin,' " 1909, pp. 49–50. "His observation and study of Nature led him to the conviction that large variations, although abundant, were rarely selected, but that evolution proceeded gradually and by small steps,—that it was 'continuous' and not 'discontinuous.' " In answer to this opinion of the most eminent British exponent of pure Darwinism it may be said that *small steps are discontinuities.* (H. F. O.)

[4] Osborn, H. F., "Darwin's Theory of Evolution by the Selection of Minor Saltations," AMER. NATURALIST, Vol. XLVI, No. 542, 1912, pp. 76–82.

[5] In 1909 L. Plate showed clearly that the "mutations" of De Vries are practically identical with the "individual differences" of Darwin. See "Darwinismus und Landwirthschaft," Berlin, 1909.

others which are obviously reversional. That he believed in the adding up of minor saltations there can be no question; but on the admirable ground that no evidence had been adduced in nature of evolution by *major saltations,* he rejected St. Hilaire's hypothesis of the natural appearance of entirely new types of animals and plants, or of new or profoundly modified organs; there was no evidence in 1872 and there is none to-day of the sudden appearance in nature of such a breed as the short-legged Ancon sheep. Morgan remarks,[6] "Darwin undoubtedly supposed that by the continuous selection of minor saltations a character could be slowly shifted in the direction of Selection. This also appears to be the opinion of the conservative mutationists of the present day."

Aside from his chief emphasis in the selection of "individual differences" Darwin also undoubtedly believed in the selection of *heritable fluctuations of proportion* as illustrated in his classic rebuttal of Lamarck in respect to the long neck of the giraffe:

> So under nature with the nascent giraffe, the individuals which were the highest browsers, and were able during dearths to reach even an inch or two above the others will often have been preserved; for they will have roamed over the whole country in search of food. These slight proportional differences will favor survival and will be transmitted to offspring.

If unusual length of neck in the giraffe, as in man, is a saltatory and heritable character, there is no reason why this classic case also may not strengthen the opinion that Darwin was essentially a mutationist. Fluctuations of proportion, the transmission of which is now in dispute, however, formed a small part of Darwin's scheme, nor was fluctuating variability especially connected by him with the process of evolution.

A very critical reexamination of Darwin's works leads us, therefore, to largely dissent from the influential opinion of De Vries[7] that there was always a doubt

[6] Morgan, T. H., letter, January 11, 1912.

[7] De Vries, Hugo, "Die Mutationstheorie," Leipzig, 1901, p. 24.

in Darwin's mind as to whether "the selection of mutations" or "the selection of extreme variants" played the greater part in the origin of species. As above noted, the actual cases which Darwin cited and his repeated emphasis shows that minor saltations of the De Vries type were chiefly in his mind.

It is obvious that Darwin could not draw such sharp distinctions either in language or in definition as we may to-day, profiting by forty years of experiment and of analysis.

Let us therefore closely examine the kinds of saltation or discontinuity in mammals which have been recorded during the last fifty years by Darwin, Bateson and others and see what they signify.

### 1. *Major and Minor Saltations in Mammals as Supposed Material for Selection*[8]

The above exposition of Darwin has a very direct bearing on the problem of continuity and discontinuity because the saltations which he believed to be among the possible materials of natural selection and of evolution were chiefly drawn from the very same sources of evidence, namely, hybridization and artificial conditions of environment, which are now drawn upon by the adherents of discontinuity; the only difference is one of degree, not of kind. The great saltatory characters of Darwin cited below (Table I) in mammals are no more profound than those cited by De Vries as composing the supposed "elementary" species of *Œnothera*. It is therefore interesting to compare twenty distinct types or forms of *major and minor* saltation in eleven different types of mammals. Our authorities are Allen, Azara, Bateson, Brinkerhoff, Castle, Darwin, Davenport, Haecker, Percival, Poulton, Ridgeway, Root, Seton, Sutton, Twining. The accompanying table presents at once the very impressive result obtained by this comparison.

[8] The writer is greatly indebted to Dr. Charles B. Davenport, of the Carnegie Institution Station for Experimental Evolution, and to Professor T. H. Morgan, of Columbia University, for criticism and suggestion on this section.

TABLE I

COMPARATIVE TABLE OF SALTATIONS

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Man | Horses | Cattle | Sheep | Deer | Pigs | Dogs | Cats | Rabbits | Guinea Pigs | Mice |
| 1. Proopic brachycephaly, abbreviation of face | | | × | | | | × | | | | |
| 2. Sudden development of horns on hornless races | | × | | | | | | | × | | |
| 3. Absence of horns on horned races | | | × | × | | | | | | | |
| 4. Supernumerary horns on horned races | | | | × | | | | | | | |
| 5. Absence of 1 horn on horned races | | | | | × | | | | | | |
| 6. Jaw appendages | × | | | × | | × | | | | | |
| 7. Taillessness, absence of caudals | × | × | | × | | | | × | | × | |
| 8. Earlessness, absence of the external ear | | | | | | | | | | | |
| 9. Single ears, loss of one ear | | | | | | | | | × | | |
| 10. Short-leggedness, or limb abbreviation | | | × | × | | | × | | | | |
| 11. Consolidation of paired hoofs, syndactylism | | | × | | | × | | | | | |
| 12. Polydactylism | × | × | × | × | × | × | × | × | | × | |
| 13. Epidermal thickenings | × | | | | | | | | | | × |
| 14. Mottled skin markings | × | × | × | | | × | | | | | |
| 15. Excessive hairiness, or length of hair | × | × | × | × | | | × | × | × | × | |
| 16. Hairlessness, entire absence of hair | | × | × | | | | × | | | | × |
| 17. Excessively fine or silky hair | × | | × | × | | | | × | × | | × |
| 18. Reversed hairs | | | × | | | | | | | × | |
| 19. White hair locks | | | | | | | | | | | |
| 20. Curled-hair | × | × | | × | | | × | | | | |
| 3a. Duplication of horns (transverse) | | | | × | | | | | | | |

The very uniformity of the result makes us suspicious as to the significance of saltations, major or minor, in evolution. In eleven different kinds of mammals, namely, man, horses, cattle, sheep, deer, pigs, dogs, cats, rabbits, guinea pigs, mice, we observe that saltations exactly or closely similar repeatedly occur. These saltations are of the same kind, in fact, they partly include those which were regarded by Darwin as possibly part of the evolution process through selection, namely, as stable in inheritance and as under certain circumstances favoring the animals which possessed them.

We evidently have to do with abnormal disturbances of the germinal factors or determiners. Some of these saltations are very stable in heredity and certain of them become widespread; some are prepotent and dominant, others are recessive (*e. g.*, angora, or "long coat" in rabbits, Castle); some (*e. g.*, bent tail in certain mice,

Plate) follow neither the Mendelian law nor the principle of blended inheritance.

On the unit-character doctrine we know that one of three things is happening in the germ plasm.

First, a "determiner" may drop out and we see a race of mammals springing up without tails, or color, or hair. In cattle the determiner for horns is dominant, therefore something is added.

Second, a "determiner" may be suddenly lost or modified, and we see excessive hair, curly hair, silky hair, dwarfed or short limbs, brachydactylism.

Third, and even more inexplicable, there occurs the appearance of a new "determiner" or the removal of an "inhibitor" and we observe horns suddenly arising on hornless races like horses and rabbits.

That fancy breeds can be established through the abnormal behavior and selection of these "determiners" there is no question. That nature works through the sudden appearance of new and favorable "determiners" is as yet unproved; it is absolutely disproved in the case of horns, for through paleontology we know that horns arise in a continuous manner. The only mammal known to us at present in which it would appear that a duplicate horn may have sprung into existence through saltation is *Tetraceros*, the four-horned antelope of India. Saltation is possibly of significance in the case of the sudden alteration of hair character because we know of a very considerable number of curly-haired horses in Mexico and South America, which are, however, eliminated by breeders for the reason that correlated with curliness of the hair are apt to arise certain other characters in the hoofs and limbs which are unfavorable.

Under wild or natural conditions in mammals we have as yet secured no direct evidence of such origins or establishment of saltations either major or minor. There is reason to believe that peculiar or anomalous mammals if they do arise are driven away from the herds.

It would appear that the obvious abnormality of the

majority of these characters throws the remainder as well as saltatory new characters in general under suspicion of abnormality.

Paleontology, however, furnishes the most direct evidence of the abnormality of saltations in some of the hard parts shown in Table I by presenting counter evidence that such profound changes as abbreviation of the face (proopic brachycephaly), development or loss of horns, reduction or absence of caudal vertebræ, abbreviation or elongation of the limbs, syndactylism or consolidation of separate metapodials have all been established, wherever we know their history, through continuity and not through discontinuity.

### 2. *Bateson's Evidence (1894) of Discontinuity*

Bateson in 1894[9] was the first to clearly advance the discontinuity hypothesis as a mode of origin of species in its modern form. At the time this work appeared it suffered a searching review from Scott.[10] Mutationists,[11] however, still refer to it as laying the foundations for the discontinuity hypothesis. In order to test the "*Materials for the Study of Variation*" critically in the light of the subsequent advance in paleontology, Dr. W. D. Matthew, who is without bias in the question, was requested to examine all the cases of discontinuity in mammals cited by the author with reference to the question whether or not these cases have any real significance in evolution. He reports:

> Of the 320 cases of discontinuity cited in mammals the greater part are obviously teratological and have no direct significance in relation to paleontologic evolution except for a very few instances such as the supernumerary or fourth molar teeth of *Otocyon*. While not significant [in evolution] these teratological cases are interesting because they show the prevalence of homœosis, and indicate that many of the

[9] Bateson, Wm., "Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species," Macmillan & Co., London, 1894.

[10] Scott, W. B., "On Variations and Mutations," *Amer. Jour. Science* (3), Vol. XLVIII, 1894, pp. 355–374.

[11] Darbishire, A. D., "Breeding and the Mendelian Discovery," 8vo, Cassell & Co., London, 1911.

remaining cases which might [otherwise] be considered normal saltations or reversions may actually be teratologic, but disguised by homœosis; all of the possibly significant cases (such as the supernumerary molars) are thereby placed under suspicion. Setting aside this suspicion the minority of the "significant" cases in teeth and feet may be said to afford evidence of the meristic variability of vestigial and rudimentary structures. Bateson's statement that such variability is related not to non-functionalism but to terminal position in a series appears to me directly in conflict with his [Bateson's] own evidence, as it certainly is with all my experience. This accords with commonly observed data in paleontology, for no paleontologist would question that vestigial teeth or bones are apt to [finally] disappear by "discontinuous" evolution. *As to the appearance by saltatory evolution of new and primarily functional parts in teeth or feet, I know of no adequate paleontologic evidence in its favor.* It is either demonstrably false or decidedly improbable. In the cases of supernumerary teeth (*Otocyon myrmecobius,* Cetacea, etc.) saltatory evolution may be regarded as reasonable in default of any paleontologic evidence to the contrary. Meristic or numerical evolution in fully functional vertebræ is intrinsically probable as the only method of evolutionary change.

The fact that so many cases of supernumerary teeth are associated with asymmetry throws doubt on the significance of all such cases; asymmetric variations and those occurring only in upper or only in lower teeth have no analogy in paleontology; such cases as occur abnormally are recognized as of a different and non-significant class than normal evolutionary changes.

A summary of Matthew's report is as follows:

Bateson cites 323 cases of discontinuity in vertebræ, teeth and skull. Of these 286 are abnormal, or teratological, or reversional, and have absolutely no significance in evolution; ten cases of supernumerary (or fourth molar) teeth are possibly significant because among the mammals there are a few genera with fourth molars which may possibly have arisen by saltation. There remain only thirty-seven cases which may be ranked as "probably significant," and these are the meristic additions or reductions of vertebræ in the spinal column, significant because of the well-known variations in the vertebral formulæ of different mammals, and secondly because vertebræ can be added or subtracted only discontinuously.

SUMMARY OF BATESON'S 323 CASES

| | | Non Significant | Possible Significant | Variations Vestigial or Reversional |
|---|---|---|---|---|
| I. | Vertebræ | 17 (asymmetry) | 27* | |
| II. | Teeth | 83 | 10† | 67 |
| III. | Feet | 110 | | |
| | | 210 | 37 | 67 |

* Numerical variations of cervical, dorsal and lumbar vertebræ.

† Additional molars, cf. *Octocyon, Myrmecobius, Cetacea.* Six cases insufficiently described.

The fact that the vast majority of germinal anomalies examined in the above review of Darwin and of Bateson have no significance in evolution in a state of nature, throws all germinal anomalies under suspicion as natural processes, important as they may be in artificial breeding and hybridizing. Yet some of these anomalies in mammals are less profoundly discontinuous than those which De Vries has cited in plants under the designation of "mutations." The most important of these De Vries' mutations may now be considered.

### 3. *Evidence for De Vries's Mutation Theory*

In 1901 the biological world was aroused as it had not been since 1859 by the publication of De Vries's hypothesis.[12] Here was a new and apparently sure foundation for discontinuity in the supposed sudden appearance of *elementary species* or "mutants" arising with the acquisition of entirely new characters, new forms of plants or animals quite free from their ancestors and not linked to them by intermediates. The influence and vitality of this great work is shown in a citation from Darbishire (1911, *op. cit.*, p. 5):

> The view that species have originated by mutation is based on Prof. de Vries' observations on the Evening Primrose (*Œnothera Lamarckiana*) (Fig. 1). Working with this form, he was able to witness, for the first time, the actual process of the origin of new species.

[12] De Vries, Hugo, "Die Mutationstheorie," Leipzig, 1901, p. 24.

Critical analysis during the past two years by Davis and by Gates[13] of the very species *Œnothera Lamarckiana* on which De Vries chiefly based his monumental work, tends to show that *O. Lamarckiana* is possibly a hybrid of *O. biennis* and *O. grandiflora* and not a natural species. Thus the "elementary species" which are springing from it in various gardens may prove to be comparable to the familiar results of hybridization in mammals and birds.

Davis, on the basis of his prolonged experimental researches, says:

> Indeed, the theory of De Vries may fairly be said to rest chiefly upon the behavior of this interesting plant, the account of which forms so large a part of his work "Die Mutationstheorie" (2 vols., Leipzig, (1901). . . . In a brief perusal of the work one is struck by the optimism of its author and the brilliancy and breadth of his exposition of the views set forth. . . . The analysis of the data amassed by Darwin, in which it is shown that Darwin's "single variations" are the same as De Vries's mutations seems to the reviewer particularly effective. . . . Probably the time will soon come when nearly all biologists will be ready to admit that mutation or the sudden appearance of new forms has been an important factor at least in species formation of plants and animals. Admitting this it remains to be discovered what relation these sudden appearances bear to *the general trends of evolution which are apparent in so many phylogenies* [italics our own] . . . for granting the facts of mutation we have only accounted for a micro-evolution, and it is still to be shown that the larger tendencies can be sufficiently accounted for by the same means without the intervention of other factors. . . .

The skepticism of both these botanists is striking. Their opinions as to the existence of larger evolutionary trends are exactly in accord with those of paleontologists.

### 4. *Evidence for Discontinuity from Mendelian Heredity and Experimental Selection*

The newest bulwark of the discontinuity hypothesis is that erected since 1903 by the revival of the great dis-

[13] Davis, Bradley Moore, "Genetical Studies on Œnothera. II. Some Hybrids of *Œnothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*," AMER. NATURALIST, Vol. XLV, April, 1911, pp. 193–233. Gates, R. R., "Mutation in Œnothera," AMER. NATURALIST, Vol. XLV, No. 538, October, 1911, pp. 577–606.

covery of Mendel (1865) and by the negative results of experiments on fluctuating or quantitative variation.

From the prevalence of discontinuity in heredity, the separateness of "unit characters" as they appear in the body and the equally sharp separableness of their complex of "factors," "determiners" or "genes" in the germ has arisen the theoretical assumption of *the discontinuity of origin of all characters in the germ.* We shall now show that this assumption is a *non-sequitur.*

First, however, the truly marvelous and epoch-making Mendelian discoveries require our especial examination in their bearing on the problem of continuity and discontinuity. We have reviewed[14] the contributions of Allen, Bateson, Castle, Cannon, Cuénot, Darbishire, Davenport, Durham, Farrabee, v. Guita, Haacke, Hagedoorn, Harmon, Hurst, Laughlin, Morgan, Pearson, Plate, Punnett, and Rosenoff. This review covers unit characters only as observed in mammals, to which none the less the principles discovered by Mendel in the common garden pea (*Pisum sativum*) apply with striking uniformity.

The prevailing field of the researches of these talented investigators in mammals has been in color characters, chemical in essence, in various species of rodents, chiefly mice and guinea pigs, also in Ungulates, such as horses and cattle, the latter studied less by experiment than from stud books. Hair form in rodents and in man and skin pigment have also been exactly investigated. The most striking general result is the principle of antithesis of characters which mutually exclude each other, as typified by the antithesis of Mendel's "tallness" and "shortness" in peas.

The second great feature is that when these antithetic characters meet in the germ cells, one dominates over the other; this dominance is a sort of perpetual prepotency. "Prepotency," observes Darbishire, "is an attribute of individuals and capricious in its appearance. . . . Whatever be the nature of this power . . . it is clear that it

[14] With the aid of Miss Mary M. Sturgess, now attached to the Carnegie Institution Station for Experimental Evolution at Cold Spring Harbor, L. I.

has nothing to do with dominance . . . dominance is an invariable attribute of particular characteristics.'"[15] Plate (1910), on the contrary, observes, "But a variety of facts seem to indicate that a reversal of dominance may occur under certain circumstances and a dominant character may become recessive, and *vice versa.*"[16] Such reversal of dominance would appear to be the case in a comparison of the mule (cross between ass ♂ and horse ♀) and the hinny (cross between the horse ♂ and the ass ♀).

When antithetic characters or functions meet in heredity, there is either "prepotency," or "dominance," or "recession" (*i. e.*, latency), or "inhibition," a something which indirectly prevents the appearance of characters, or "imperfect dominance," or "blending." In brief, there are *degrees* of separableness and antithesis.

*Dominance, Conservative or Progressive.*—It will be seen at once that progressive evolution through discontinuity would depend on the *dominance of racially new characters and types.* The experimental evidence is conflicting, it does not show that new characters are necessarily dominant.

There are many instances of dominance of wild species (older type) over domesticated species (newer type); thus De Vries suggested (1902) that the dominant characters are those which are racially older. One case among the mammals is that the wild gray color in mice dominates over grades below it, black, brown, and white (Plate, 1910).

Examples of dominance in single characters are that more intense dominate over less intense colors (Plate, 1910, Davenport, 1907); in the eyes, brown over gray, gray over blue; in the skin, brunettes over blondes (Davenport, 1909), piebalds over pure albinos (Plate, 1910). In the hair, wavy or spiral forms dominate over straight (Davenport, 1908). This would have some bearing on the discontinuous fading out of color in desert races like the quagga, which lost all the stripes of its relative the zebra.

[15] Darbishire, *op. cit.*, p. 96.

[16] Plate.

The idea that the positive or present character dominates over the negative, latent or absent character has become the prevailing one.

It seems highly probable, observes Davenport (1910), that the future will show that many more advanced or progressive conditions are really due to one or more unit-characters not present in the less advanced condition. In that case it will appear that there is a perfect accord in the two statements that the progressive and the "present" factor are dominant (pp. 89–90) . . . the specific characteristics are mostly those that appear late in ontogeny (p. 86) . . . the potency of a character may be defined as the capacity of its germinal determiner to complete its entire ontogeny. If we think of every character as being represented in the germ by a determiner, *then we must recognize the fact that this determiner may sometimes develop fully, sometimes imperfectly and sometimes not at all* [italics our own]. . . . When such a failure occurs in such a normal strain a sport results. . . . Potency is variable. Even in a pure strain a determiner does not always develop fully and this is an important cause of individual variability (Davenport, 1910, p. 92).

Plate similarly favors the hypothesis of dominance of newer or progressive characters. He observes (1910):

The [Mendelian] laws of inheritance favor progressive evolution in two ways, for . . . higher, more complicated characters are generally dominant to the lower, and . . . qualitative characters usually follow the Mendelian principle in the case of closely related forms (races, varieties) while in the crossing of species they follow intermediate [or blended] inheritance as a rule. In the latter case there is the possibility that the crossing may have a swamping effect, but this can play no large rôle on account of the infrequency of hybrids between species (Plate, 1910, p. 606).

The same author is of the opinion that phyletic evolution is discontinuous as regards the transformations of the determinants [determiners], but in most cases is continuous in their visible outward workings. He thus maintains that while germinal transformations are discontinuous there may be no real antithesis between continuous and discontinuous somatic variation.

Thus Mendelians appear to agree, *first,* that there are *grades of continuity and discontinuity,* that there are antithetic characters which are sharply discontinuous, others which are partly continuous, blended or intermedi-

ate. *Second,* it would appear that complete discontinuity or entire dominance or recession are qualities in heredity *which may gradually evolve.* Many characters show imperfect dominance (Castle, 1905); gametic purity is not absolute (Castle, 1906); selection is of importance in the improvement of races (Castle, 1907). There are a number of truly blending characters, such as lop-earedness in rabbits (Castle, 1909), cross blends of long and short hairs (Castle, 1906), cross blends between short- and lop-eared rabbits which are permanent (Castle, 1909), blends in weight inheritance and in skeletal proportion (Castle, 1909).

More recent work has tended to show (Hatai, 1911)[17] that blended inheritance may be considered to be a limited case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard in all the cases referred to it (Hatai, 1911, p. 106). Certain characters which were considered formerly to blend are now regarded as showing a certain kind of segregation or unit inheritance. Thus Davenport (1909) observes:

> Skin pigment does not show thorough blending inheritance, but segregation (sometimes imperfect), a more pigmented being imperfectly dominant over a less.[18] . . . The reason, the same author observes (1909, for the blending of hair and skin color in man is the non-development of distinct color unit-determiners owing to the fact that in man for a long period there has been no selection for intensity of color, whereas in the lower mammals definite color determiners have long been maintained by selection.

Thus the prevalent recent opinion among Mendelian observers is *that there is a real discontinuity between the germinal or blastic characters and what the paleontologist or morphologist generally observes, is only an apparent continuity between somatic characters.*

[17] Hatai, Shinkishi, "The Mendelian Ratio and Blended Inheritance," AMER. NATURALIST, Vol. XLV, No. 530, February, 1911, pp. 99–106.

[18] Pigmentation of the skin seems to depend in man on a series of color intensity units, possibly one or a few large units, more probably a number of small units so close together as to be almost continuous (Davenport, 1910).

Since, however, the behavior of somatic characters forms our only means of knowing whether the determiners are continuous or discontinuous, it is obvious that this opinion requires further examination in the conceptions of Johannsen.

### 5. *Johannsen's Pure Line Theory*[19]

The theoretic contrast between the real discontinuity of the blastic determiners and the delusive continuity of visible or somatic form is pushed to its extreme in the "pure-line" conception which marks the latest development in heredity, an advance upon Weismann's germ-plasm theory and Mendel's unit-character law. Through experiments on successive generations of self-fertilizing plants (the garden bean), Johannsen has reached a standpoint which may be briefly stated as follows:

A "pure line" is composed of the descendants of one pure strain or homozygotic organism exclusively propagated by self fertilization; such pure lines demonstrate the stability of hereditary constitution in successive generations where undisturbed by cross breeding or mingling with other strains, showing that the only real changes in organisms are those due to the sudden appearance of new determiners in the germ.

To replace the word *determiner* the term *gene* is proposed. The *genotype* represents the sum total of all the genes in the fertilized germ cell, gamete or zygote: we do not know a genotype but we are able in experiment to demonstrate "genotypical differences." The *biotype* is a group of similar genotypes or pure strain individuals.

Gene, genotype, and biotype are not seen; they are the smaller and larger units of heredity.

The phenotype is what we see; it is the developing organism. Morphology supported by the huge collections of the museums has operated with "phenotypes" in phylogenetic speculation. It is thus a science of phenotypes and is not of value in genetics because phenotype description is inadequate as the starting point for genetic inquiries. The adaptation of phenotypes through the direct influence of environment [Buffon's factor] or of use and disuse [Lamarck's factor] is not of genetic importance. Ontogenesis is a function of the

[19] Johannsen, W., "The Genotype Conception of Heredity," AMER. NATURALIST, Vol. XLV, No. 531, March, 1911, pp. 129–159.

genotype, but the genotype is not a function of ontogenesis. The idea of evolution by continuous transitions from one type to another has imposed itself upon zoologists and botanists, who are examining chiefly shifting phenotypes in very fine gradations. There is such a continuity in phenotypes but not in the genotypes from which they spring. All degrees of continuity between phenotypes may be found, but real genetic transitions must be distinguished from the transitions which we find in museums.

Genotypes, it is true, can only be examined by the qualities and reactions of the phenotypes.

Such examination shows that within pure lines—if no new mutations or other disturbances have been at work—there are no genotypical differences in the characters under examination. The only real discontinuity is that between different genotypes. The mutations observed in nature have shown themselves as considerable discontinuous saltations. There is no evidence for the view that mutations are practically identical with continuous evolution. In pure lines no influence of special ancestry can be traced; all series of progeny keep the genotype unchanged through long generations. Discontinuity between genotypes and constant differences between the genes show a beautiful harmony between Mendelism and pure line work.

Selection will have no hereditary influence in changing genotypes. Even the selection of fluctuations in pure lines is ineffective to produce a new genotype.

Heredity may thus be defined as the presence of identical genes in ancestors and descendants, or heredity stands for those properties of the germ cells that find expression in the developing and developed phenotype.

Similarly Jennings observes:[30] What distinguishes the different genotypes, then, is *a different method of responding to the environment*. And this is a type of what heredity is; *an organism's heredity is its method of responding to the environmental conditions* [p. 84]. . . . It appeared clear, and still appears clear, that a very large share of the apparent progressive action of Selection has really consisted in the sorting over of preexisting types, so that it has by no means the theoretical significance that had been given to it [p. 88]. . . . I had hoped to accomplish this myself, but after strenuous, long-continued and hopeful efforts, I have not yet succeeded in seeing Selection effective in producing a new genotype. This failure to discover Selection resulting in progress came to me as a painful surprise, for like Pearson I find it impossible to construct for myself a "philosophical scheme of evolution," without the results of Selection and I would like to see what I believe must occur [pp. 88–89]. . . . It would seem that the diverse genotypes must have arisen from one, in some way, and when we find out how this happens, then such Selection between genotypes

will be all the Selection that we require for our evolutionary progress [p. 89].

Thus Johannsen's general conception of the origin of progressive or retrogressive new characters is that "it is sufficient to state that the essential point in evolution is the alteration, loss or gain of the genes or constituents of the genotype . . . all evidences as to 'mutations' point *to the discontinuity of the changes in question.*"

### 6. *Negative Results of Experiments on Quantitative Variation*

We agree with Johannsen that a delusive *appearance* of continuity might arise through selection of degrees of hereditary fluctuation in structure or function, for example, of tallness or shortness of stature, of intensity or faintness of color. Some Mendelians discard fluctuations altogether as non-hereditary; thus Punnett (1911, p. 138)[20] observes: "At the present time we have no valid reason for supposing that they [fluctuations] are ever inherited."

The question, however, is not as to quantitative ontogenic variations caused by favorable or unfavorable environment or by changes of habit, but as to heritable fluctuations springing from the germ plasm. Experiments have been directed to the point whether variations in size, in proportion, etc., of unit characters as distinguished from the unit characters themselves are transmitted.

Davenport has reached negative results; he observes (1910):

> In the last few decades the view has been widespread that characters can be built up from perhaps nothing at all by *selecting in each generation the merely quantitative variation that goes farthest in the desired direction.* The conclusion upon which De Vries laid the greatest stress, that quantitative and qualitative characters differ fundamentally in their heritability, is supported by our experiments (p. 96). I have made two tests of this view using the plumage color of poultry

[20] Punnett, R. C., "Mendelism," Macmillan Co., 1911 (3d edition).

(p. 94). . . . After three years of selection of the reddest offspring no appreciable increase of the red was observed except in one case, which looks like a sport (p. 96). These fluctuating quantitative conditions depend on variations in the point at which the ontogeny of the character is stopped; and the *stopping point* is in turn often if not usually determined by external conditions which favor or restrict the ontogeny. Thus the selection of redness of comb, of polydactylism, of syndactylism, have not proved the inheritance of quantitative variations. Apparently, within limits, these quantitative variations have so exclusively an ontogenic signification that they are not reproduced so long, at least, as environmental conditions are not allowed to vary widely.

Similarly Love[21] from experiments on the yielding power of plants remarks:

Unless further studies produce different results we can say from the facts at hand that there is no evidence to show that a basis exists for cumulative selection.

Similar conclusions have been reached by Pearl (1909)[22] in the breeding of fowls for laying purposes.

All the above results are negative.

Even the positive or affirmative results obtained by Cuénot and later by Castle, wherein quantitative characters may be shifted in one direction or the other by selection are now given a new interpretation by certain Mendelians. For example, Cuénot showed by continued selection of lighter colored mice that the coat became paler; and Castle has shown that in rats the coat through selection may be made darker. Castle remarks (1911):[23]

I prefer to think with Darwin that selection . . . can heap up quantitative variations until they reach a sum total otherwise unattainable, and that it thus becomes creative.

He cites cumulative results in the development of a fourth toe in the hind foot of guinea-pigs and in the modification of the dorsal striping of hooded rats.

[21] Love, Harry H., "Are Fluctuations Inherited?" Contr. VI, Lab. Experim. Plant-Breeding, Cornell Univ., AMER. NATURALIST, Vol. XLIV, No. 523, July, 1910, pp. 412–423.

[22] Pearl, Raymond, "Is there a Cumulative Effect of Selection?" Abstammungs- und Vererbungslehre, 2, 1909, H. 4.

[23] Castle, W. E., "The Nature of Unit Characters," The Harvey Lectures, delivered under the Auspices of the Harvey Society of New York, 8vo, J. B. Lippincott Co., pp. 90–101.

Morgan's remarks (1912) on these positive experiments are as follows:

> Castle has been very guarded in regard to the *interpretation* of the results of selection in this case. It is probable that extreme selection is necessary to maintain the higher stage reached. It does not breed true and slips back easily. If this is correct it suggests: first, that nothing permanent has been effected in the germ-cells; and second, that the result is due to the discovery of more extreme cases of fluctuating variations than ordinarily occur.

The general import of these experiments and opinions is that fluctuations in the determiners, or genes, can not be utilized to establish a new quantitative mean. It is obvious that what have been measured by biometricians as hereditary "fluctuations" might be regarded as "saltations" of all degrees, but such saltations do not represent *new* determiners in the Mendelian or Johannsen sense; they are mere fluctuations in existing determiners. Pure Mendelians would allege that tallness in man or other mammals can only be accumulated through the saltatory origin of "tall" determiners which are not connected continuously through intermediate forms with the antithetic "short" determiners. As to stature Brownlee observes (1911, p. 255):[24]

> I think that I have shown that there is nothing necessarily antagonistic between the evidence advanced by the biometricians and the Mendelian theory. . . . (1) If the inheritance of stature depends upon a Mendelian mechanism, then the distribution of the population as regards height will be that which is actually found, namely, a distribution closely represented by the normal curve.

### 6. *Summary as to Discontinuity and Mendelism*

Genetics is the most positive, permanent and triumphant branch of modern biology. Its contributions to heredity are epoch-making. But heredity is the conservative aspect of biology, and experimental genetics thus far reveals the laws of conservation.

[24] Brownlee, J., "The Inheritance of Complex Growth Forms, such as Stature, on Mendel's Theory," *Proc. Roy. Soc. Edinburgh*, Vol. XXXI, Pt. II, 1911, pp. 251–256.

Genetics has not yet brought us one single step nearer the solution of the problem of the progressive origin of new characters in mammals. The very independence, multiplicity and discontinuity of the units leave us farther afield. In place of what used to be regarded as the instability of the organisms, as a whole, we now have to conceive of the instability of thousands, nay hundreds of thousands of units.

As shown in our analysis of the saltations cited by Darwin and Bateson, Mendelism has revealed the fact that the majority of saltations simply reflect failures in the germinal mechanism. The inference is natural that the remaining minority also represent anomalies, or lawless conditions. Over a half century of anatomical research among mammals has failed to demonstrate in a state of nature the sudden origin of a single new progressive character which has become fixed in the race.

Nor have Mendelism and experimentalism released us from the hard confines of examination of the germ through the soma; behavior of unit characters in the soma is the sole means of knowing the behavior of the "determiners" in the germ. If the unit characters in the soma behave discontinuously we are forced to the conclusion that their determiners behave discontinuously; if, on the contrary, these unit characters behave continuously, are we not forced to the conclusion that there is a continuity in the behavior of the corresponding determiners?

Let us therefore proceed to consider the value of some of the evidence for continuous behavior in the origin of certain new characters, again repeating our opinion that certain other characters are antithetic, without intermediates, and consequently discontinuous both in heredity and in origin.

*(To be concluded)*

## THE BOTANICAL SOCIETY OF AMERICA

At the Washington meeting of the Botanical Society of America, the following papers constituting a symposium on Modern Aspects of Paleobotany were read by invitation of the council, on December 28th.

I. "The Relations of Paleobotany to Geology."
F. H. KNOWLTON.

II. "The Relations of Paleobotany to Botany."
1. "Phylogeny and Taxonomy." JOHN M. COULTER.
2. "Morphology." EDWARD C. JEFFREY.
3. "Ecology." ARTHUR HOLLICK.

In accordance with the instructions of the Society these papers are here printed in full.

GEORGE T. MOORE,
*Secretary*

## MODERN ASPECTS OF PALEOBOTANY

### I. THE RELATIONS OF PALEOBOTANY TO GEOLOGY

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ALTHOUGH there is vague mention of fossil plants in literature as early as the thirteenth century, and unscientific adumbrations in the faintly growing twilight of the succeeding centuries, the real science of paleobotany did not have its beginning until well on in the nineteenth century. With the publication, in 1828, of Brongniart's "Histoire des végétaux fossiles" and the "Prodrome," there was given to paleobotany "that powerful impetus which found its immediate recognition and called into its service a large corps of colaborers with Brongniart, rapidly multiplying its literature and increasing the amount

of material for its further study." Ward. In the succeeding decades, even to the close of the century, the students of paleobotany were mainly occupied in accumulating data as regards distribution, both areal and vertical, and the opening decades of the present century find the subject a recognized, respected, coequal part of the general field of paleontology.

Paleobotany, together with all the other branches of paleontology, admits of subdivision into two lines or fields of study—the biological and the geological—depending upon the prominence given to the one or the other of these phases of the subject. The biological study is, of course, concerned especially with the evolution of the vegetable kingdom, that is, with the tracing of the lines of descent through which the living flora has been developed. As this side of the question will be taken up by other contributors to this discussion, it may be dismissed from further consideration, as the geological aspect is almost exclusively the phase of the subject to which the present paper is devoted.

In the first place it will be necessary to call attention to the fact that the successful use of fossils of any kind as stratigraphic marks is—or at least may be—entirely independent of their correct biological interpretation. To most botanists, and indeed to some paleobotanists, this statement will doubtless come as a surprise, since they have come to imagine that the impressions of plants, the form in which they are most made use of in this connection, are so indefinite, indistinct and unreliable that they can not be allocated biologically with even reasonable certainty, and hence are of little or no value. As a matter of fact hardly anything could be further from the truth, and it can be confidently stated that it makes not the slightest difference to the stratigraphic geologist whether the fossils upon which he most relies are named at all, so long as the horizon whence they come is known and they are clearly defined and capable of recognition under any and all conditions. They might almost as well

be referred to by number as by name, so long as they fill the requirements above demanded, though of course every stratigraphic paleontologist seeks to interpret to the very best of his knowledge the fossils he studies. He may—doubtless often does—make mistakes in his attempts to understand them, but his errors are undoubtedly fewer than he is not infrequently charged with! His faculty of observation is rendered acute from the close study of the restricted and often fragmentary material available, and he has learned to see and make use of characters which are often overlooked or wholly neglected by the botanist. The latter, even when he has before him the complete living plant, including root, stem and foliar and reproductive organs, sometimes experiences difficulty in correctly placing his subject, and, to judge from some recent work, there are paleobotanists who study only the internal structure of fossil plants and yet are beset with extreme difficulty in interpreting their biological significance.

It may then be taken as settled that the needs of the stratigraphic geologist will be met if he is supplied with a series of marks or tokens by which he may unfailingly identify the various geological horizons with which he deals, while to the historical geologist who makes use of fossils in unraveling the succession of geological events, the correct biological identification is of the greatest importance, for upon this rests his interpretation of the succession of faunas and floras that have inhabited the globe. As the late Dr. C. A. White has said: "If fossils were to be treated only as mere tokens of the respective formations in which they are found, their biological classification would be a matter of little consequence, but their broad signification in historical geology, as well as in systematic biology, renders it necessary that they be classified as nearly as possible in the manner that living animals and plants are classified."

While it is in no way desired to overlook or underestimate the biologic value of such fossil plants as have for-

tunately retained their internal structure in condition for successful study, it is probably safe to say that their value to geology as compared with the impressions of plants is as 1,000 to one, and had we only the former, there never could have been developed the science of stratigraphic paleobotany. For example, the collections of the U. S. National Museum embrace over 100,000 specimens of the impressions of Paleozoic plants, whereas of those showing internal structure there is hardly a half dozen unit trays full. In the Mesozoic and Cenozoic collections belonging to the same institution there are thousands upon thousands of specimens from hundreds of localities and horizons, while of those retaining their internal structure there are so few that they can almost be numbered in tens.

There is another and an excellent practical reason why the impressions of plants are, and will always remain, of more value to geology than those exhibiting internal structure, no matter how well this structure may be preserved. As soon as a plant impression is exhumed it is instantly ready for study and may be interrogated at once as to the stratigraphic story it has to tell, whereas the plant with the structure preserved usually shows little or nothing on a superficial examination, and requires laborious, expensive preparation before it can be identified. For example—to make a personal application—for the past five years I have annually studied and reported on from 500 to 700 collections, each of which embraced from one to hundreds of individuals, and with them have helped the geologists to fix perhaps fifty horizons in a dozen states. If it had been necessary to cut sections of these specimens before the geologist could have had his answer, it is safe to say that very little would have been accomplished.

All fossil plants must be interpreted by and through the living flora. In the more recent geological horizons the plants are naturally found to be most closely related to those now living, but as we proceed backward in time

the resemblances grow less and less and finally we find ourselves in the presence of floras a large percentage of which are without known or clearly recognized living representatives. In describing these and making them available for stratigraphic use it has been necessary to give them generic and specific names, after the analogy of the living floras, so that we may have convenient handles by which to use them. Many of these are confessedly what may be called genera of convenience, such, for example, being many of the genera of the so-called "ferns" of the Paleozoic. Some—but especially botanists—unfamiliar with the geological use of fossil plants, have argued that it is unsafe, or even actually unwise to venture to give names, not only to those without living representatives, but even to those obviously belonging to living groups. A reply to this objection seems unnecessary in view of what has been said.

The practical application of fossil plants as an aid to geology may be briefly mentioned. There have been described from—let us say—North America, upwards of 5,000 species, of which number some 1,200 are confined to the Paleozoic, perhaps 2,000 to the Mesozoic, and 1,500 to the Cenozoic. During the sixty or seventy years that this information has been accumulating it has developed that certain species or other groups enjoy a considerable time range, and therefore are of little value in answering close questions of age, while others are of such limited vertical distribution that their presence may indicate instantly a definite horizon. Thus, if he find in association impressions that we have named *Sequoia Nordenskiöldi, Thuya interrupta, Populus cuneata,* etc., it is known instantly that we are dealing with the lower Eocene Fort Union formation, since not one of these species, together with several hundred others, has ever been found outside this horizon. Innumerable other concrete examples could of course be given, though hardly necessary, yet it may be instructive to note that within a single geographic province—the Rocky Mountain region—the several plant-

bearing formations present are characterized as follows: The Kootenai by 120 species, the Colorado by perhaps 50 species, the Dakota by 460 species, the Montana by 150 species, the Laramie by 140 species, the Arapahoe by 30 species, the Denver by more than 150 species, the Fort Union by from 500 to 700 species, etc., etc. This shows that, as Professor J. W. Judd once said: "We still regard fossils as the 'Medals of Creation,' and certain types of life we take to be as truly characteristic of definite periods as the coins which bear the image and superscription of a Roman emperor or of a Saxon king."

Just a word may be said on the economic application of stratigraphic paleontology. It is perhaps safe to say that never in the history of American geology has there been so close an interrelation and dependence of geology on paleontology as at present, and of this confidence paleobotany may justly claim its full share. Thus, of the even dozen of paleontologists in the employ of the U. S. Geological Survey and covering all branches of the subject, four are paleobotanists.

Among the many subsidiary problems connected with the application of paleobotany to geology, the use of fossil plants as indices of past climate occupies a most important place. As the majority of plants are attached to the substratum and hence are unable to migrate like most animals when the temperature of their habitat becomes unfavorable, they must either give way or adapt themselves gradually to the changed conditions of their environment. Therefore, fossil plants have always been accorded first place as indices of past climates. "They are," as Dr. Asa Gray has said, "the thermometers of the ages, by which climatic extremes and climate in general through long periods are best measured."

To those who have not given especial consideration to the subject, the idea appears to obtain that climatic variations, such as now exist, are normal or essential and that they were present without marked differences during all geological ages. It is now established, however, that this

conclusion is entirely without geological or paleobotanical warrant, and that the most pronounced climatic differentiation the world has known extends only from the Pliocene to the present. As a matter of fact we of to-day are living in the glacial epoch in what possibly is only an interglacial period, and we know that the time which has elapsed since the close of the last ice-invasion has been of less duration than was one, and possibly two, of the Pleistocene inter-glacial periods. We also know that the climate was milder during these inter-glacial intervals than has obtained since the final retreat of the ice, as shown by the fact that in eastern North America certain species of plants then reached a point some 150 miles further north in the Don Valley than they have since been able to attain. The development of strongly marked climatic zones, at least between the polar circles, is, then, "exceptional and abnormal, and we have no evidence that in any other post-Silurian period, with the possible exception of the Permo-Carboniferous period, has the climatic distribution and segregation of life been so highly differentiated and complicated as in post-Tertiary times."[1]

The regular and normal conditions which have existed for vastly the greater part of geologic time, have been marked by relative uniformity, mildness and comparative equability of climate. This is abundantly shown by the almost world-wide distribution and remarkable uniformity of the older floras. When, for instance, we find the middle Jurassic flora extending in practical uniformity from King Karl's Land, 82° N., to Louis Philippe Land, 63° S., we have conditions which not only bespeak a practically continuous land-bridge, but exceptionally uniform climatic conditions. To have made this possible there could have been neither frigid polar regions nor a torrid equatorial belt, such as now exist. The absence of growth-rings in the stems of these plants, as well as the presence of such warmth-loving forms as cycads and tree-ferns, point to the absence of seasons and the presence of mild and equable climatic conditions.

[1] See White and Knowlton, *Science*, N. S., Vol. 31, 1910, p. 760.

Another example of similar import is afforded by the early Pennsylvanian flora, that is, the flora of the lower part of the Upper Carboniferous. Wherever terriger-ous beds of this age have been discovered, representatives of this peculiar flora, which includes such common genera as *Lepidodendron, Sigillaria, Sphenophyllum,* etc., have been found, this distribution ranging from South Africa to Brazil and Argentina, and thence over the northern hemisphere.

Similarly, the Mississippian flora (Lower Carboniferous) has been found in Spitzbergen, Greenland and arctic Alaska, and thence south over Europe and America, and although somewhat older than the last, is distinctly related to that in Argentina.

On passing up in the geologic time scale we find that during late Mesozoic and early Cenozoic time the present dominant types of vegetation were firmly established. With what probability of success may these floras be interrogated as to the climatic conditions under which they existed? We find from a study of the present flora that certain types of vegetation, as well as certain plant associations, have definite climatic requirements. Thus, *Artocarpus,* or the bread fruit trees, are now confined to within 20° of the tropics, showing that they require the moist heat of the torrid regions. If, now, we find that *Artocarpus* once throve in Greenland 70° or more north, during Cretaceous time, we feel justified in assuming that its climatic requirements were not very different from those of its living representatives. And when we find that it was then in association, as it is to-day, with cycads, tree-ferns, cinnamons, palms and other distinctly tropical forms we are confirmed in the opinion that at that time Greenland must have enjoyed a tropical or at least a sub-tropical climate.

Another example is afforded by the Fort Union formation. In the rocks of this horizon, which now occur on the wind-swept, almost treeless plains of the Dakotas, Wyoming and Montana and thence northward to the val-

ley of the Mackenzie, are found remains of *Sequoia, Taxodium, Thuya, Ulmus, Populus, Vitis, Platanus, Sapindus, Viburnum, Corylus, Juglans, Hicoria,* etc., etc. From this array we feel justified in assuming a cool to mild temperate climate for this early Eocene flora, and further, from the presence of numerous, often thick beds of lignite, that there was a much higher precipitation than at present.

A layer of fan-palm leaves a foot in thickness in a formation in northern Washington indicates climatic requirements in which the minimum temperature did not fall below 42° F. The presence of numerous West Indian types in the Miocene lake beds of Florissant, Colorado, would alone point to almost tropical conditions, but as these are associated with others of more northern affinities, it seems safe to predicate at least a warm temperate, or possibly sub-tropical climate.

## II. The Relations of Paleobotany to Botany

### 1. *Phylogeny and Taxonomy*

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It is impossible to disentangle morphology and phylogeny, for the largest motive in modern morphology is to construct phylogenies. An excessive amount of overlapping will be avoided in this paper by laying the emphasis upon the inferences to be drawn from morphological investigations as to probable lines of descent, rather than upon the morphological results themselves.

It should be kept clearly in mind that the material of paleobotany, as indicated by the program, is not always used to contribute to the science of botany. The determinations of plants in the interest of geological horizons are of immense service to geology, but of comparatively little value to botany. This means that some paleobotanists are geologists, and some are botanists, and it is the work of the latter that concerns us at this time.

The recent rapid development of our knowledge of the structures of fossil plants is familiar to botanists, constituting as it does one of the most remarkable chapters in the history of our science. This has been due not only to the elaboration of a technique for sectioning petrifactions, but also to the inclusion of the vascular system among the morphological material that is recognized to be significant in conclusions concerning phylogeny. From the standpoint of paleobotany, the vascular system is its most valuable asset for vascular plants, for its chances of preservation exceed those of any other structures except the seed, and its significance in phylogeny is far more apparent and extended than that of the seed. As a result of this paleobotanical connection, the phylogeny of the vascular groups can be made now a resultant of comparative structures and actual history. Many an old phylogeny, based upon the comparative structures of existing plants alone, has been contradicted by history, which, in the nature of things, must furnish the final check upon any proposed phylogeny.

The topic of this paper is really an invitation to indicate some of the recent reactions of modern paleobotany upon the phylogenies of vascular plants. The title includes taxonomy, but in so far as this deals with great groups, defined or discovered, it is covered by the statements concerning phylogeny. So far as it deals with the recognition of individual forms, it is clear that paleobotany must learn to recognize the relationships of fossil plants, or there will be no reliable taxonomy or phylogeny. So long as paleobotany depended upon the form resemblances of detached organs, there could be no taxonomy in the real sense. It was merely a cataloguing of plant material. But when it learned to uncover structure, it began to establish a real taxonomy. The contributions of paleobotany to taxonomy, therefore, may be summed up in the statement that it has begun to extend our schemes of classification into the ancient floras; that this has resulted in a far truer view of the great groups

than their expression in the present flora can possibly give; and that this makes a rational phylogeny possible.

I will address myself in the main, therefore, to phylogeny, as involving all the taxonomy that is of large importance. When paleobotany to-day assembles the great series of paleozoic pteridophytes, the impression is very different from that of a few years ago. It is true that we have always heard of the giant forms of the Paleozoic and their dwarf representatives of to-day. We contrasted *Lepidodendron* with *Lycopodium,* and *Calamites* with *Equisetum,* and the total impression was the striking difference in size.

Now we have learned that these paleozoic Lycopodiales and Equisetales were not merely comparatively large, but that they were also comparatively complex. For example, we have learned that their huge bodies developed secondary wood and had attained heterospory. We begin to understand that vascular plants, with the exception of Angiosperms, were as completely differentiated, so far as the great groups are concerned, at the beginning of our records as now; and that the phylogeny in sight is not that of one great group following another, but of all the great groups spraying out into more and more modern expressions.

Not long ago, our morphology taught that the homosporous *Lycopodium* is the modern representative of the arborescent, paleozoic club mosses, and that the heterosporous *Selaginella* is a modern offshoot. Now we find that the paleozoic forms, with their heterospory, their ligules, and their other structures, link up with *Selaginella;* and we are asking, where are the ancestors of *Lycopodium?* Not long ago *Isoetes,* once suspected of being responsible for the monocotyledons, was fluttering between Filicales and Lycopodiales, and at last had settled down as an anomalous member of the latter group; and now modern paleobotany assures us that its whole structure suggests that it is a much reduced and compacted *Lepidodendron.* Thus the anomalous *Isoetes* has a ten-

tative connection, and the very normal *Lycopodium* has none.

Once we talked of the evolution of the strobilus as shown by *Lycopodium, Selaginella,* and *Equisetum,* and fancied that we saw in these modern forms the highest expression of the pteridophyte strobilus. Now we know that these strobili of to-day are excessively simple as compared with those of the Lycopodiales and Equisetales of the Paleozoic. The evolution of the pteridophyte strobilus that is in sight, therefore, is an evolution from a complex strobilus to a simple one.

According to the old morphology of external form, the club mosses were entirely capable of having given rise to the conifers. With some knowledge of structure this idea faded away, except in certain quarters, and the brilliant discovery of the so-called "seed-ferns" seemed to dispose of it entirely. Now we find among the paleozoic lycopods, notably some of the herbaceous ones, that a seed-like structure has been attained, and we have "seed-club mosses" as well as "seed-ferns." This does not mean that the club mosses gave rise to conifers or to any other existing group of seed plants, for more important structures forbid it; but it does mean that the paleozoic groups had advanced very far; that the seed-condition may have been attained by several groups of paleozoic pteridophytes; and that it takes more than a seed to distinguish a "seed-plant."

These are a few illustrations of the upsetting facts that modern paleobotany has been introducing into the old-time phylogenies of Lycopodiales and Equisetales.

It is among the phylogenies of Filicales, however, that modern paleobotany has wrought the greatest change, so far as pteridophytes are concerned. The old picture included a luxuriant fern vegetation during the Paleozoic, which culminated in the Coal-measures, whose so-called "fronds" made up at least one half the vascular flora. The occasional attached synangium or sorus was plainly like those of the Marattiaceæ, and since the *Marattias*

are eusporangiate, these paleozoic ferns were eusporangiate. And so we settled back comfortably to the conviction that the paleozoic ferns were Marattiaceæ, represented to-day by a small tropical family; that the eusporangiate habit and synangia are historically older conditions than the converse; and that the leptosporangiate habit and sori of free sporangia are comparatively modern.

The change of view that modern paleobotany has introduced must be familiar to most of you. The abundant fern vegetation of the Paleozoic has vanished, having been replaced by a great group of fern-like gymnosperms; many of the marattiaceous synangia have proved to be the microsporangiate structures of these same gymnosperms; there is no indication that the eusporangiate habit is older than the the leptosporangiate; and it is entirely clear that our earliest known ferns had free sporangia and not synangia. In fact, after the first revulsion of feeling, following the discovery of the fern-like gymnosperms, the question was seriously raised, is there any evidence of paleozoic ferns? Of course no one doubted their existence, but where is the evidence?

Paleobotany has now begun to answer this important question. Evidence of the existence of a group of arborescent, *Marattia*-like ferns during the Upper Carboniferous is accumulating. Much of this evidence is negative, for it consists simply of the fact that many species of certain of the large, so-called "frond genera" have not been found to be fern-like gymnosperms. On the doctrine of chance this may be worthy evidence. It simply means that a vast display of fern-like leaves must contain some ferns. The positive evidence, however, is supplied by vascular anatomy, and is found in the stems called *Psaronius*. The structure of these stems has been compared recently with the very characteristic structure of the stems of the living marattias, and the close relationship is obvious. Moreover, the leaves of *Psaronius* belong to one of the largest frond genera, and some of them bear

*Marattia*-like synangia. So clear is the evidence that Scott has called these arborescent *Marattias,* of the later Paleozoic, Palæo-Marattiaceae, and they may well stand for the precursors of the much humbler *Marattias* of to-day.

But these ancient *Marattia*-like forms were not the oldest ferns, for paleobotany has revealed a much older assemblage of undoubted ferns, so old, in fact, that the assemblage is called Primofilices. They are represented not only by numerous detached sporangia, many of which have the annulus characteristic of modern leptosporangiates, but all the essential structures of one well-characterized family, the Botryopterideæ, are known. These still somewhat vague Primofilices are extremely suggestive and perplexing. The free sporangia and the annulus of the Botryopterideæ suggest leptosporangiate connections; but the sporangia are not borne as among the leptosporangiates, nor is the annulus of the same character. The sporangia are in clusters terminating the bare branches of a rachis; and the annulus is a vertical, multiseriate band on one side or both sides of the sporangium. In fact, the so-called "rudimentary" annulus of *Osmunda* suggests a reduced multiseriate annulus of one of the Botryopterideæ. The vascular system, however, is very characteristic and very primitive, and is so varied as to suggest a synthetic type that might have given rise to all the diversities found in modern ferns.

The possibilities of paleobotany are well shown in connection with these Primofilices. One of its form-genera, *Stauropteris,* known only as sporangia, has been discovered by Scott with germinating spores. The germination of a fern spore is so different from that of a microspore of gymnosperms, or of any other heterosporous plant with which we are acquainted, that it is clear that *Stauropteris* is a fern sporangium and not the microsporangium of some gymnosperm. When germinating spores are preserved, and also the swimming sperms of paleozoic gymnosperms, as recently described, we may expect

that paleobotany will presently be able to uncover all of the essential morphology of the great fossil groups.

This picture of paleozoic ferns is somewhat dim yet, but were it not for the recent work in paleobotany we should have no picture at all, or, what is worse, an entirely false one.

The most conspicuous contribution of modern paleobotany, however, is its remarkably complete reconstruction of the phylogeny of gymnosperms. Our present records of this group extend through a longer period and are more continuous than for any other vascular group. It was not only associated with the paleozoic pteridophytes of the Coal-measures, but it was contemporaneous with pteridophytes throughout all their recorded history. Seed-plants, therefore, are just as old as any vascular plants, so far as our records go. It is clear that seed-plants have descended from pteridophytes, but when our records begin, they had already descended.

Our conception of gymnosperms before the paleobotanical work of the last decade, will emphasize the change that has taken place. We thought of them as cycads, conifers, and gnetums; and the morphology of that time undertook to develop a phylogenetic sequence with these three groups. Cycads were clearly the most primitive gymnosperms, and when *Ginkgo* was found to share with them in the retention of swimming sperms, it was just as clearly a "transition" form, on its way from cycads to conifers. In the dim paleozoic background Cordaitales lurked, but they were quite detached from living gymnosperms, a group that belonged to the gelogist rather than to the botanist. I fancy that many a student of gymnosperms in those distant days never even heard of Cordaitales. The contrast between such a perspective of the group as I have just indicated and the perspective we possess to-day is due almost entirely to paleobotany.

In the first place, it resurrected the most primitive group of gymnosperms, the Cycadofilicales, called by our English brethren the Pteridosperms. It is a group that

had always been with us, disguised as paleozoic ferns, and the story of its recognition and rehabilitation is about the most sensational one in the annals of paleobotany. This meant that Cordaitales had a companion group, and that there were two great gymnosperm assemblages during the Paleozoic. Then the question arose as to the relationship of these two groups. There was no historical sequence to answer the question, for the two groups were observed side-by-side, and very distinct, as far back as the records go. This threw the answer back upon comparative structures, and this testimony is clear. If the two groups have been derived from ancient ferns, and the structure of Cycadofilicales hardly admits of any other conclusion, it is evident that the Cordaitales have departed much further from that origin. Therefore, if the two groups are related to one another genetically, and the discovery at various paleozoic horizons of persisting synthetic forms that combine features of both groups seems to make this reasonably assured, the Cordaitales were derived from Cycadofilicales older than any we know.

The beginning of our perspective, therefore, is that very ancient ferns, earlier than any of our records of vascular plants, gave rise to a Cycadofilicales stock, which persisted throughout the Paleozoic; and that this stock, also earlier than any of our records, gave rise to the Cordaitales branch. The records begin with these two stocks working along towards their modern expression, and all Mesozoic and modern gymnosperms can be referred to them. In other words, the gymnosperm genealogical tree comes into sight as two strong branches of a dichotomized trunk whose existence and character are hypothetical.

The Mesozoic branches from these two paleozoic stocks furnish us with another triumph of paleobotany, and this achievement is of peculiar interest to Americans.

The Cycadofilicales of the Paleozoic contributed to the Mesozoic the gymnosperms once known as "fossil cycads," a group so dominant and so characteristic that the

Mesozoic was long called "the age of cycads," so far as its vegetation is concerned. These characteristic Mesozoic forms are known now as the Bennettitales, and their resurrection from rich Mesozoic deposits of America is due to the skill and patience of our American colleague, Dr. Wieland. They retained many of the primitive features of the Cycadofilicales, but departed from them chiefly in the development of a strobilus. Not only so, but the strobilus is peculiar among gymnosperms, all of which have strobili except the fern-like Cycadofilicales. The strobilus of Bennettitales is bisporangiate, and the two sets of sporophylls are related to one another as they are in the flowers of Angiosperms. With the investment of sterile bracts, the strobilus as a whole bears a remarkable structural resemblance to such a flower as that of *Magnolia*. This resemblance has proved to be very seductive, for it has led to the claim that Bennettitales represent the ancestral forms of angiosperms. It is not the province of the present paper to discuss this claim. It has in it as a basis just enough of structural resemblance and of historical timeliness to make a plausible argument, but hardly enough to carry conviction to those who must take other facts into consideration. In any event, the Bennettitales are a notable group, and paleobotany has revealed them to us.

Along with them, the true cycads, or Cycadales, began to appear, apparently never a dominant group, and they have persisted in the tropics to the present time. The cycads as we know them, therefore, are the modern representatives of an old phylum, which included Bennettitales in the Mesozoic and Cycadofilicales in the Paleozoic, a phylum aptly called the Cycadophytes. The cycads present us with that paradox with which students of phylogeny are familiar, namely, they are structurally very primitive, but historically modern. So far from being the oldest of living gymnosperms, they are younger than the conifers and the ginkgos.

The Cordaitales of the Paleozoic had already developed

strobili, and had made notable changes in the vegetative body, changes which characterize the second great gymnosperm phylum, fittingly called the Coniferophytes.

The connections of the paleozoic Cordaitales with the Mesozoic ginkgos and conifers are very obvious, and these two groups, associated with Bennettitales and some Cycadales, made up the mesozoic gymnosperm flora. The Ginkgoales are really a mesozoic type, for their representation to-day by a single species is probably due to preservation by culture. It is an interesting fact that the ginkgos, directly connected with the paleozoic Cordaitales, have retained the primitive reproductive structures of that group and of the Cycadophytes, but advanced in vegetative structures as did the conifers. The group is very old in its reproductive methods, and modern in its vegetative body.

The great gymnosperm group of the Mesozoic, as of the present time, is the Coniferales, and their deployment during the Mesozoic is a subject of fascinating interest. The so-called tribes of conifers are found distinctly differentiated during the Mesozoic, and the determination of their relative ages is one of the triumphs of vascular anatomy. My colleague in this symposium, Professor Jeffrey, has lived in the storm center of this work, and it would not be fitting for me to invade his own special field. It may be said, however, that to discover that the Abietineæ (the pine tribe) are the oldest conifers is upsetting the older phylogeny fully as much as paleobotany has done for other gymnosperm groups.

The conifers are distinguished among the other gymnosperms that have been discussed, in being modern both in reproductive methods and vegetative structure. In contrast with cycads, therefore, they present the same paradox conversely, that is, they are structurally younger than cycads, but historically older.

This hasty outline of gymnosperm history, which paleobotany has interpreted for us, proves convincingly that no plant phylogeny is adequate until it has included

the historical record, which of course is the province of paleobotany; and furthermore, that general conclusions based upon the study of the living flora alone are more apt to be false than true.

The great problem of paleobotany to-day is the history of angiosperms. Having perfected a weapon in the attack upon gymnosperms, it remains for the paleobotanist who is a vascular anatomist to uncover the origin of our greatest group, with its comparatively brief history. The origin is probably recorded in the Mesozoic, and we wish to see the significant structures, and not guess at external form, and much less guess at purely hypothetical connections. To this great task paleobotany is turning. We have had the guesses; and I am confident that presently we shall have the facts.

## II. The Relations of Paleobotany to Botany

### 2. *Morphology*

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The morphology of Goethe's metamorphoses, a hundred years ago, was entirely external morphology, illuminating at the time and for many decades later; but now for over a quarter of a century extinct, except so far as it lives on for descriptive purposes in manuals of systematic botany. It has been replaced by a conception of morphology, based not on external form but on internal structure. The replacement has been slow in this country, where, unfortunately, morphology is still very largely a thing of external threads and patches. The father of plant morphology in its modern form, was, as you all know, Wilhelm Hofmeister, who, over fifty years ago, began to put the subject on a truly evolutionary basis. Like many other men of genius, he was before his time and received little appreciation from his less progressive contemporaries.

But it is Professor Coulter's task to deal with morphology, particularly in its paleobotanical aspects, in relation to systematic botany, as is specially fitting, since the laboratories over which he presides at Chicago have up to the present time been the greatest single influence in putting American morphology on a modern and progressive basis. His important relation to systematic development in this country is also well known, representing as it does an earlier but not less striking phase of his botanical activity. My excuse for even referring to systematic matters in these preliminary remarks is the close relation in which they necessarily stand or should stand to morphology and paleobotany. Darwin in his immortal "Origin of Species," although but little given to figurative language, has described morphology as the soul of natural history. It is to be feared that there is just ground for complaint, that the botanical natural historian has in the past too often worn his soul upon his sleeve or has even appeared to lack that necessary adjunct of higher existence. Internal morphology now holds the field and all other lines of botanical activity from systematic botany to plant physiology must take account of its doings, if they are to make solid and enduring progress.

If a change has come in recent years in the point of view of morphology, an equally important shifting of position has taken place, during the past few decades in the attitude of paleobotany. Until the late seventies of the nineteenth century, paleobotany had to do practically with the external form of plants alone, as they appear as impressions in the rocks. It is true that Brongniart in the earlier years of the last century realized the importance of internal structure in the case of fossil plants and, as Dr. Scott has recently pointed out, his views on this subject are so clear and fit actual conditions so well, that they read as if they were written only yesterday. But Brongniart had few followers even among his own countrymen. To the Englishman, Williamson, belongs a large

part of the credit of putting paleobotany on a really satisfactory footing. He insisted on the absolute necessity of taking into consideration internal structure as well as external form, and went so far in some of his writings as to state that imprints or impressions alone, of extinct plants, had little scientific value. What may be called the evolutionary bias of Englishmen, a fortunate inheritance from the greatest of all biologists, Charles Darwin, has led them far in the pursuit of paleobotany on anatomical lines. We need only call to mind the demonstration on anatomical grounds that the greater part of the trees of the Coal Period were, in spite of their arboreal habit, in reality vascular cryptogams, a demonstration absolutely confirmed later when it was possible to study, in detail, their reproductive organs. An even more striking illustration of the same kind is supplied by some of the fern-like forms of the Paleozoic, which have long appeared in the catalogue as vascular cryptogams. Here too it was first shown on anatomical grounds, and afterwards from the examination of the organization of the reproductive structures, that outward appearances were entirely deceptive and that the organisms in question were in reality seed plants of a primitive type. These two illustrations, which might be indefinitely multiplied, serve to indicate the very important services which the study of internal organization has rendered both to the natural system and to the doctrine of evolution. They further make it clear that the aphorism of mundane existence, which admonishes us not to trust to appearances, holds equally well in the domain of plants. Paleobotany, like morphology, has accordingly at the present time entered into the anatomical phase of development.

So long as morphology concerned itself mainly with the external form of the reproductive structures of existing plants and paleobotany had perforce to content itself for the most part with the impressions upon the rocks of the foliar organs of extinct ones, there was little to

bring these two branches of botanical science together. The systematic botanist was accordingly quite safe in ridiculing the insufficiency of the evidence upon which the conclusions of the older paleobotany was founded. With the advent of the anatomical phase of development in both morphology and paleobotany, the two sciences have become united on the basis of common interests and are both enormously strengthened by the union. Morphology, from being the exponent of *a priori* philosophical ideas, applied to the question of the evolution of plants, and derived for the most part from the inner consciousness rather than from any truly scientific and inductive study of facts, has become the logical fancy-free handmaiden of evolution. Paleobotanical science, on the other hand, having realized, especially in the case of the older plants, which are naturally of the greatest importance from the evolutionary standpoint, that the external form, even the external form of the reproductive structures, is often very deceptive as to real affinities, has come to regard as most important the much less variable internal organization of extinct plants. Paleobotany is in the position to supply us now, for the first time, with reliable facts regarding the organization and true systematic affinities of the ancient vegetation of the earth, and morphology has reached a condition of maturity where facts are infinitely more important than philosophical fancies, however charmingly expressed.

It is unfortunately the case that morphology, until comparatively recently, has been quite as unscientific in its methods as the systematic botany with which in the earlier years of its existence as a branch of botanical science it was intimately allied. The recent important change of attitude in plant morphology is practically entirely due to extensions in our knowledge of the organization of extinct plants. Sachs in the second part of his classic "History of Botany," which deals with plant anatomy and similar matters, deplores this unsatisfactory condition in the following words: "Owing to the ex-

traordinary diversity of opinion that exists among botanists even on the most general questions in the science, it is extremely difficult to ascertain what can be considered a common possession,—an unfortunate condition of things from which no science suffers perhaps so much as Botany." Until comparatively recently these words were as true of plant morphology and plant physiology as when they were written, nearly forty years ago. If there is any mitigation of the situation it is because of the application of chemical and physical laws to the understanding of the functioning of plant structures and the facts of modern paleobotany to the elucidation of the structures themselves. There can be no doubt whatever, that, without the background supplied by our increasing knowledge of fossil plants, the picture painted by the morphologist and embryologist of the evolution of plants is without depth and entirely without perspective. We literally can not see our wood for the countless trees which have crowded into the foreground representing its most modern stage of development. It is certainly impossible to formulate even the rudiments of the evolutionary perspective of plants in the absence of paleobotanical facts as the enduring and fundamental background.

It is accordingly impossible to deny that in the past morphology has been largely fanciful, where it has departed in any way from the bare description of the facts of structure in modern plants, or has attempted to arrange them in accordance with any general or scientific principles. True the situation has been relieved not a little, as a result of the study of development and comparative anatomy, but the difficulty has always been here to decide the direction in which a comparative or developmental series should be read. The indispensable sense of direction can alone be supplied by sighting down the fingerposts of the past, the records of fossil plants, which show us the real path by which evolutionary advancement has been made in any given case.

One of the commonest fallacies of the older morphology was to regard simpler structures as more ancient and complicated ones as more specialized and modern. This error is very deeply implanted in the existing highly artificial systematic arrangement of the higher plants. For example in the case of the conifers, the Taxaceæ are put lower than the Pinaceæ, on account of the simpler organization of their reproductive and vegetative structures. The paleobotanical record, however, shows us clearly that the Pinaceæ, particularly the abietineous Pinaceæ, are among the most ancient representatives of the coniferous stock, while the Taxaceæ, particularly the genus *Taxus,* stand for the class in its most modern condition of development. Let us take another illustration from the Angiosperms. Systematic text-books invariably place the Monocotyledones below the Dicotyledones, on the basis of their simpler organization. This view of the matter does not accord, however, with the results of anatomical and paleobotanical research, which clearly show that the Monocotyledones are neither ancient in their occurrence nor primitive in their organization, but represent a condition of reduction from ancestors which were essentially dicotyledonous in their more important characteristics. These two illustrations, which might be multiplied indefinitely from systematic works, show that the older morphology was essentially fanciful and philosophical in its methods and by no means worthy of the name of an inductive science.

The new morphology, purely inductive in its procedure, is solidly founded on the testimony of the rocks and considers no sequence valid, unless it is clearly supported by the evidence derived from the study of fossil forms. It shows itself moreover scientific in its firm adhesion to valid general principles and its disregard of uncoordinated facts. These general principles too are few in number and are as easily grasped in their simplest form as are the great generalizations of the sister sciences, chemistry, physics and

astronomy. The three most important laws or general principles of morphology are those which have to do with recapitulation, reversion and retention. The first is common to both plants and animals, while the other two are infinitely better illustrated by botanical than zoological facts. The validity of these laws has long been admitted in a somewhat hazy and unpractical fashion. It has remained for morphology based on paleobotany to bring them into prominence as the fundamental working principles of the investigator of plant evolution. They are in fact the rudiments, the three R's of biological science, with which even the tyro should become well acquainted.

We can not do better than take a particular illustration of these laws as applied to botanical facts. The conifers show themselves particularly favorable for the elucidation of general evolutionary principles, because they not only constitute a large, varied and widely distributed element of our existing flora, but can be traced, with trifling interruptions, continuously far into the past. Of the conifers there is one tribe at the present time entirely confined to the southern hemisphere. I refer to the Araucariineæ, of which the New Zealand Kauri and the Norfolk Island pine may appropriately stand as examples. In the Mesozoic period, the middle ages of our earth, they flourished throughout the entire world. It is often considered that the Araucariineæ represent the most ancient group of conifers. This belief appears to be based on a too common fallacy, that groups nearly extinct in the existing flora necessarily represent ancient forms. A further basis for the hypothesis of the extreme antiquity of the Araucarian conifers is derived from their habit and the general features of organization of their wood, in both of which respects they present points of resemblance, by no means complete, however, with those Paleozoic gymnosperms to which the origin of the general coniferous class is by common consent of morphologists and paleobotanists referred, namely, the Cordai-

tales. If we follow the Araucariineæ backward step by step, as recent additions to our knowledge now permit us to do, into the past, we find that although in the Tertiary they retained very largely the characteristics which they present to-day in the Cretaceous, particularly in the Lower Cretaceous and in the Jurassic, they become less and less like their existing representatives and more and more like the Abietineæ, the actually dominant conifers of the northern hemisphere, both in general organization and wood-structure. To save time let us consider only three points of anatomical organization, for comparison. The existing Araucariineæ are remarkable among conifers and gymnosperms generally, in possessing leaf-traces which continue to be formed in the wood by the cambium, long after the leaves which they originally supplied have ceased to exist. The old trunk of a *Kauri* or an *Araucaria,* for example, shows on the outside of its wood marks representing the traces of leaves, which may have disappeared hundreds of years previously. This feature has been seized upon by Professor Seward as one of undoubted primitiveness. It is certainly bizarre, and if one accepts the unusual as the criterion of antiquity, the Araucariineæ certainly could qualify for an ancient lineage on this character. This view does not however accord with paleobotanical facts. In the Lower Cretaceous we find very many undoubted Araucarian trunks, in which the leaf-traces were not persistent as in the existing representatives of the tribe and in the Jurassic and Triassic trunks of this type become practically universal. This at once makes it clear that the persistent leaf-trace, so characteristic of the living *Kauri* and *Araucaria,* is not an ancestral feature of the Araucarian stock. Recently we have sent out from Harvard a botanical expedition to Australasia. At my suggestion Messrs. Eames and Sinnott, who were its personnel, have brought back old seedlings of the two existing Araucarian genera. On investigation of the lower region of these in proximity to the cotyledons, it

was found that here the leaf-traces were ephemeral in their persistence, exactly as in the older Mesozoic representatives of the Araucarian stock from the Lower Cretaceous, Jurassic and Triassic deposits. Here appears a very striking example of the validity of the law of recapitulation as exemplified by the young individual, the seedling stem for a short part of its vertical length repeating ancestral conditions which have long disappeared in the adult. Let us consider two remaining characters together, in order to economize time. The water pores of the tracheids in existing Araucarian conifers occur in a crowded and alternating condition and are deformed or flattened by mutual contact, a feature of resemblance to the oldest known gymnosperms. This feature is in marked contrast to the pit arrangements of the other existing tribes of conifers, where the water pores are loosely grouped and when numerous and multiseriate are opposite. Another unusual feature of the wood of existing Araucariineæ is the absence of wood parenchyma, a feature likewise illustrated by the woods of the Paleozoic gymnosperms. If we follow the Araucarian conifers below the horizon of the present, we observe in the older representatives a condition of pitting of the tracheids, which the lower we go geologically, becomes more and more like that found in the other tribes of conifers, particularly the Abietineæ, so much so that Gothan, who has recently described the Jurassic woods of Spitzbergen and other arctic islands, which in the Mesozoic supported a luxuriant flora, has identified them as of Abietineous affinities. It is further found in the case of those Mesozoic fossil woods which most nearly resemble the living genera *Agathis* and *Araucaria,* that wood parenchyma was exceedingly abundant. Now let us examine our Araucarian seedlings in regard to these features. The wood of the cotyledonary region here exemplifies both the characteristic pitting and presence of wood parenchyma of the Mesozoic *Araucarioxylon* type. Thus the Araucariineæ, which we are able to follow very

far back into the past, present a very striking illustration of the biological law of recapitulation. Other features of the seedling might have been considered with the same result.

But ancestral conditions are not in plants confined to the young individual. We find them also illustrated in connection with the principles of retention and reversion. The law of retention is well exemplified by the root, cone and first vegetative annual ring of the Araucariineæ, where the Mesozoic features of structure appear only less completely than they do in the seedling. The law of reversion is likewise illustrated readily in this tribe of conifers in connection with injuries, for the wood formed subsequently to wounds shows Mesozoic characters, which are not a feature of normal structure.

It appears clear from the illustration which I have chosen, only one among many possible ones from the results of recent coordinated anatomical, developmental, experimental and paleobotanical investigations, that we have definite laws of plant evolution. It is further clear that like Ulysses we must "follow knowledge like a sinking star" into the night of the past, if we are to reach durable general biological principles. The laws of recapitulation, retention and reversion, founded on cases where it is possible to trace an unbroken sequence of forms, are likewise applicable to the elucidation of conditions in groups the past of which is as yet insufficiently known. A very notable example of this kind is presented by the Angiosperms. Here more than anywhere else among the higher plants philosophical views in regard to evolution prevail. You are doubtless all familiar with the generally accepted dictum, forming a feature of all elementary botanical instruction, that the woody stem of perennial Dicotyledones is derived from one of herbaceous texture. This conclusion is based on the old fallacy, that simpler conditions are necessarily antecedent to more complex ones and antedate them in time. If we investigate the primitive type of stem organization

in the Dicotyledones, in accordance with the principles of recapitulation, retention and reversion, we arrive at very different conclusions indeed and of much greater significance from the standpoint of evolution.

It will save time to take a concrete illustration. In the cross section of a small branch of the oak we find the woody part of the stem, composed of ten alternatingly outstanding and depressed segments, separated from one another by ten large so-called primary medullary rays. In accordance with the herbaceous hypothesis of the origin of the woody stem, the projecting segments are supposed to correspond to five originally entirely separate bundles. Further the intervening depressed segments of the cylinder, set off from the others by the ten large rays, are supposed to represent parts of the wood which have been secondarily interpolated through the activity of a so-called interfascicular cambium. If we examine the facts in the light of the general principles of plant evolution, a very different and much sounder conclusion is reached. Let us take only the seedling evidence, for the other accords absolutely with it. In the cotyledonary region of the young stem we find for a number of years a completely continuous woody cylinder, without either large rays or depressed segments. At this level in fact the rays are entirely narrow ones of the gymnospermous type. Both the broad rays and the segments which they delimit appear only later. The so-called large primary rays are in fact formed as a result of the fusion of smaller rays into aggregates around the incoming leaf-traces. The broad rays of the oak are consequently fusion products and not at all primitive structures. They are clearly related as a storage device for the strands which enter the stem from the leaves. There are two broad rays to each leaf, corresponding to its two strongly developed lateral traces, and since the phyllotaxy of the oak is of the 2/5 type, there are normally and originally five pairs of large rays in the stem. The depression of five of the segments delimited by the

large leaf or foliar rays below the level of their fellows presents another interesting problem in evolution, into which there is not time to enter at present. It is enough to say that the so-called primary or large rays of dicotyledonous stems are not primary or primitive structures at all, but are of secondary origin and formed from what was originally wood, in order that the assimilates from the leaves may more readily and conveniently be stored for future use. We have thus an explanation of the relation of the woody to the herbaceous stem, which is at once in harmony with the general principles of plant evolution and at the same time with physiological necessities. The fallacy of considering the herbaceous as the primitive type is further made clear. There is in fact every reason to believe that the early Dicotyledones were entirely woody perennials, just as the forbears of the existing herbaceous Pteridophyta have been shown by paleobotanical and anatomical investigations to have been derived from arboreal ancestors of the Paleozoic.

The clear realization of the universal validity of the primary laws of plant evolution depends almost entirely on our increased knowledge of the organization of fossil plants. There has come to morphology as a consequence of the study of ancient forms a new birth, quite comparable to the remarkable intellectual awakening in Europe, at the beginning of the modern period, resulting from the rediscovery of the ancient classics of the Greeks and Romans. This awakening, known as the renaissance, has its exact counterpart in plant morphology and our enthusiasm over the discovery of new fossil remains which throw a light on the origin of existing plants is not different from that experienced by the enlightened citizens of the Italian cities at the end of the middle ages, over the unearthing of a new manuscript of Virgil or of Horace. As a result of this impetus the morphologist has already in the past decade revolutionized the systematic arrangement of the Gymnosperms and the work in this special field has scarcely begun. In the case of the

Angiosperms, change is also in the air and I venture to predict that within two or three decades at most we shall have made substantial progress towards a scientific, that is, a natural, classification, of what is at present a huge and hopelessly confused labyrinth, penetrated at best in a halting way by the tenuous and insecure thread of our present highly artificial system.

The future presents many interesting possibilities for the morphologist and the paleobotanist and let us hope for the systematist as well. Obviously we are now on the threshold of the discovery of a system of plants which shall depict their evolutionary sequence. Would that we might count on the sympathetic cooperation of all systematic botanists in this stupendous and intellectually attractive task. Unfortunately in the thirties of the last century systematic botany parted company with plant morphology and has appeared since somewhat to resemble the man with the muckrake in the vision of the immortal tinker. Although there hangs above it the shining diadem of a natural system, with which to crown its arduous labors of many years, the raking together of straws, sticks and even antique dust seems to present an invincible attraction. The assiduous strokes of the rake may glean additional straws and sticks; but although we may all agree that he is a benefactor of mankind who makes two living blades of grass sprout where there was one before, we shall scarcely consent with unanimity that the making of more new species out of old ones, is a highly commendable scientific occupation. A great danger on the systematic side appears at the present time to inhere in the doings of so-called world congresses. Recently the paleobotanists of those countries which are mainly active in the investigation of fossil plants have agreed unanimously and publicly to repudiate the vote of the recent congress at Brussels, imposing upon them Latin diagnoses of extinct plants. The students of fossil plants, although they have to do with organisms no

longer living, regard their science as a live one and are consequently strongly unwilling to shroud its doings in the pall of a dead language, perhaps not the less because the mandate to do so comes as the result of a Russian ukase. The present world congresses of botanists seem to present certain ominous resemblances to the world councils of the church about the time of the Reformation in Europe. The so-called ecumenical councils of Christianity were unfortunately characterized at that time by reactionary tendencies, including among others a preference for the Holy Writ in the Latin rendering of the Vulgate. Unless there is some relaxation of the mediæval attitude upon the part of the majority of systematic botanists, there is reason to fear a reformation in botany, as uncontrollable as that led by Martin Luther and John Knox in religion. It is sometimes said in favor of Latin diagnoses of plants, that the older literature of systematic botany is in the Latin tongue. The same is true of the equally venerable sciences of chemistry and astronomy, yet for that reason the chemists and astronomers of to-day do not think it necessary to perpetuate the written language of the alchemists and astrologers. Botany has likewise, let up hope, passed through what corresponds to the alchemistical and astrological phase of development and need not conceal its doings in the dog Latin of a Paracelsus or an Albertus Magnus. Conditions in this country are hopeful in this respect, for although we are not wholly free from the pedantry that maketh and loveth a Latin diagnosis, the large majority of American systematists are entirely progressive in their point of view. May they prevail and in the course of time, with all modesty, impress their attitude on the European cultivators of this important field of botanical activity.

## II. The Relations of Paleobotany to Botany

### 3. *Ecology*

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As I understand the object of a symposium it is not to provide opportunity for the reading of exhaustive or highly technical dissertations, or for the presentation of new material, but rather to present recognized facts as clearly as may be, with recent interpretations of their meaning or significance, in order to enlist interest in and to stimulate discussion of the subject under consideration; and this seems to have been the view which was taken by those who have preceded me. In such connection it is my privilege to present the claims of ecology to recognition, in indicating the relations between botany and paleobotany.

Plant ecology, as the term is commonly defined and understood, is that branch of botany which deals with the study of the interrelations of plants and their relations to environment. As a distinct science it is practically a product of the present generation. I do not know exactly when the term was first employed in scientific literature, but it certainly was not in general use in connection with botany at the time of my earliest contributions to the subject, and I did not then know that I was dealing with ecology when discussing certain floras and their accompanying geologic and physiographic features of environment.

The ecologic relations between botany and paleobotany are mostly concerned with the problems of phytogeography. Paleobotany has supplied the explanations of numerous puzzling facts in regard to the geographic isolation of certain genera; the occurrence of some genus or species only in certain widely separated regions of the earth; and the problems in connection with many endemic floras. Indeed the phenomena of plant distribution in

general at the present time would be lacking in logical or adequate explanation but for the facts which have been brought to light by the study of fossil plants in regard to distribution in the past. Many such instances might be cited, but for the purposes of this symposium a few of the most striking only need be recalled to serve as concrete examples of the general abstract propositions.

In the earlier part of the last century, when the science of paleobotany was in its infancy, and much that we now know about living plants had not been learned, numerous remains of coniferous trees were found in Europe and elsewhere in the Old World, in deposits of relatively recent geologic age. For the most part these remains were either identified as living genera or were given generic names designed to indicate their nearest apparent relationships with such (*Pinites, Taxites, Araucarites,* etc.). Other similar remains, however, which could not be satisfactorily compared with any living ones, were given new generic names. Among these latter may be mentioned certain small cones associated with leafy twigs, which were assumed at the time to represent an extinct coniferous genus. Large areas of the New World, however, were yet unexplored and many hitherto unknown living genera were awaiting discovery and description. One of these was *Sequoia,* a genus of two species only, confined in their distribution to scattered groves on the western coast of the United States. Ecology was an unknown science when these groves were discovered, but the relatively limited number of the individual trees, and their geographic isolation, at once attracted attention and aroused interest and discussion in regard to their ancestry and the phenomenon of their peculiar distribution. Paleobotany supplied the desired information. When the generic characters of *Sequoia* were made known they were seen to be identical with those of the supposed extinct fossil coniferous genus of the Old World. Further than this, however, similar remains, comprising numerous different species, were sub-

sequently found extending through Siberia to the eastern coast of Asia and through Europe, Iceland, Greenland and the Arctic regions to Alaska, and thence southward to the home of the two remaining living species on the western coast of North America. The phytogeographic problem of the genus *Sequoia*, as we know it to-day, was thus resolved into the geologic problem of the causes which produced the climatic changes resulting in the extinction of the genus over vast areas where it formerly existed, and the total extinction of all except two of the numerous species by which it was formerly represented. Modern areal *limitation* of the genus was thus shown by paleobotany to be a result of former areal *elimination*.

(Incidentally it may be remarked that this example also involves a question of nomenclature which, however, I trust our chairman may declare to be not germane to the subject and hence ineligible for discussion. *It is one of the few instances in which a genus was known and named as a fossil before it was discovered and named in its living form.*)

The genus *Taxodium*, comprising two, or possibly three living species, is confined to the southern United States and Mexico, so far as its present distribution is concerned. Up to the close of the Tertiary period, however, it flourished throughout what are now the temperate and arctic zones of North America and Eurasia,—not only the genus, but apparently the identical species yet living and others now extinct. Paleobotany has adduced ample proof of these facts, so that, as in the case of *Sequoia*, the present distribution of *Taxodium* is explained as merely the result of its elimination from other regions where it formerly existed.

The monotypic genus *Ginkgo*, which by many is also regarded as representing a monotypic family and order, is confined, so far as its natural distribution is concerned, to eastern China and Japan. No known facts could adequately account for its taxonomic and geographic isolation until paleobotany revealed the multiplicity of its ex-

tinct specific and allied generic forms, and its former wide distribution throughout the Eurasian and North American continents.

Another monotypic living genus, *Sassafras,* limited in its present distribution to eastern North America, represents an ancient type of angiosperm vegetation whose fossil remains have been found not only throughout North America, but also in many parts of the Old World.

These are merely a few of the many examples of generic isolation—geographic and taxonomic—the explanations of which have been supplied by the study of paleobotany.

Other apparent peculiarities of distribution, such as are represented in our living flora by *Liriodendron* and *Nelumbo,* genera which are restricted to eastern Asia, eastern North America and the central American regions, are exceedingly difficult to explain satisfactorily on any theory of migration in recent times; and the theory of origin *de novo* in each of the widely separated regions is too thoroughly discredited to merit discussion. None of the known facts of recent plant migration, or evolution, or mutation, are adequate to explain the conditions as we now find them. Paleobotany, however, has demonstrated that such apparent peculiarities of generic distribution are readily explained when the facts of former distribution are ascertained. Each of these genera was formerly world-wide in its distribution and prolific in species; but changes in environment caused their extinction in all except the widely separated regions which they now inhabit, reducing the species of *Nelumbo* to two, and of *Liriodendron* to one. What have been regarded as problems of distribution, explainable by improbable theories of migration or evolution, have thus been shown by the facts of paleobotany to be merely some of the many examples of isolation due to elimination in intermediate regions.

The peculiar endemic flora of Australia did not originate *de novo* by reason of its isolation. Paleobotany has shown that the living endemic flora of Australia in many

of its characteristic elements, such as the genus *Eucalyptus,* represents what the general vegetation of the entire earth was like at the close of Mesozoic time, when the continent of Australia was isolated from the rest of the world. Elsewhere than in Australia climatic and physiographic changes subsequently eliminated the Mesozoic types of vegetation and evolved new ones; but in Australia the conditions remained almost stationary, and that continent to-day, so far as its native flora and fauna are concerned, is still in a late Mesozoic or early Neozoic stage of development. It is an endemic flora not because it has evolved new types by reason of its isolation, but because it has remained stationary by virtue of this reason, while the great bulk of the world's vegetation has changed.

And so the paleobotanist extends the right hand of fellowship to the botanist and says, "when you are puzzled, or in doubt, don't despair, come to us," for individually or collectively we can, probably, suggest reasonable explanations, not only as to why living plants have come to be *where* they are, but also how they have come to be *what* they are.

# SHORTER ARTICLES AND DISCUSSION

## THE INFLUENCE OF CAVE CONDITIONS UPON PIGMENT DEVELOPMENT IN LARVÆ OF AMBLYSTOMA TIGRINUM

One of the possible methods of approach to the problem of the origin of the modifications of cave animals is by experiments in which outside forms are kept under conditions normally encountered by animals living in caves. In following up this method of approach, it seemed best to select forms as plastic as possible (if perchance there are forms which are plastic with reference to modifications by cave conditions). Typical cave animals, *i. e.,* species highly adapted for cave life, perhaps without exception belong to families and genera having many members showing an inclination toward cave habitation either by actually frequenting or living in caves or by inhabiting similar dark and retired situations elsewhere; so that it might seem that these groups possess a certain plasticity toward modifications by cave conditions. Especially might this plasticity be expected in the particular species which already show a tendency to live under conditions resembling those of caves.

Young animals may be expected to be more responsive to changed environment than adults, and since many of the urodeles live in caves and similar situations, and their eggs and young can be obtained in numbers and reared with comparative ease, amphibian larvæ were selected for some of the experiments.

Newly laid eggs of *Amblystoma tigrinum* were collected (in some cases were laid in jars in the laboratory where some of the adults were confined) from March 30 to April 4, 1911. The eggs, in small lots, were placed in a number of 6-inch battery jars, and the jars divided into two lots, Series *A* and Series *B*. Series *A* was placed in the artificial cave while Series *B* was kept on a laboratory table adjacent to and directly in front of a west window. Otherwise the two series were, as far as possible, subjected to like conditions. Unfortunately it was not possible to keep Series *B* at as low or as uniform a temperature as Series *A*. Development was somewhat slower on the average with Series *A* than with Series *B*, and both of these developed slightly less rapidly than a third series, Series *C*, observed in the pool where the eggs were laid and the larvæ allowed to develop

under natural conditions, but as I shall attempt to show later neither temperature differences nor different rates of development materially influenced the amount of pigment developed.

The animals were fed on alternate days with an abundance of daphnids and cyclops, and later with small bits of tender beef. The amount of pigment developed was judged by making accurate determinations of the color of two definite regions of the skin of each individual. For the body color, determinations were made for a region to one side of the median line and about midway between the pectoral and pelvic limbs. This is the most heavily pigmented region of the larva. For the head color the region immediately anterior to a line from one eye to the other was used. This is usually the least pigmented portion of the animal. The colors were obtained by means of the Milton Bradley color tops and the records made in percentages of black, white, orange and yellow, which when blended most nearly matched the color of the skin of the animal. The orange used in these tops most nearly resembles the No. 101 of Klincksieck et Valette's "Code des couleurs" and the yellow is intermediate between Nos. 206 and 211. All the color records under consideration for Series *A* and *B* were made within two weeks and under uniform conditions so that the results ought to be strictly comparable. The records for the somewhat more rapidly developing Series *C* were made about three weeks earlier. The results tabulated include color records for all the surviving individuals of Series *A* and *B* and sixteen individuals selected at random to constitute Series *C*.

The average body color of the Series *A*, numbering 22 individuals, reared in the cave, contained 49.7 per cent. of black, 16.9 per cent. white, 9.3 per cent. orange and 24.1 per cent. of yellow; or 49.7 per cent. black and 50.3 per cent. non-black. The extreme range in degree of pigmentation was from 32 black and 68 non-black to, in the case of one individual decidedly darker than its fellows, 70.5 black to 29.5 non-black. The average head color was 38 per cent. black and 62 per cent. non-black (26.7 white, 7.0 orange and 28.3 yellow) with 27 per cent. and 51 per cent. as the extremes in amounts of black.

On the average, Series *B* (7 individuals), reared in laboratory light, had a body color of 86.1 per cent, black and 13.9 per cent. non-black (4.7 white, 2.4 orange and 6.8 yellow), and a head color of 76.1 per cent. black and 23.9 per cent. non-black (8.4 white, 4.0 orange and 11.5 yellow). The range for the body color was from 82 to 90.5 black and for the head color

from 62.5 to 90 black, ranges distinct from and not at all overlapping those for Series *A* reared in darkness.

Series *C* (16 individuals), living in the outdoor pool under natural conditions, had an average body color of 86.6 black and 13.4 per cent. non-black (4.5 white, 3.1 orange and 5.8 yellow), the extremes ranging from 77.5 to 93 per cent. black. The head color averaged 78.3 black and 21.7 non-black (7.7 white, 4.2 orange and 9.8 yellow) with 61 per cent. and 90 per cent. the extremes in amount of black. The data for all three series are shown together in the adjoining table.

| | Body | | | | | Head | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Black | White | Orange | Yellow | Total Non-Black | Black | White | Orange | Yellow | Total Non-Black |
| Series *A* (cave): | | | | | | | | | | |
| Extremes: | | | | | | | | | | |
| Darkest | 70.5 | | | | 29.5 | 51.0 | | | | 49.0 |
| Lightest | 32.0 | | | | 68.0 | 27.0 | | | | 73.0 |
| Averages | 49.7 | 16.9 | 9.3 | 24.1 | 50.3 | 38.0 | 26.7 | 7.0 | 28.3 | 62.0 |
| Series *B* (laboratory): | | | | | | | | | | |
| Extremes: | | | | | | | | | | |
| Darkest | 90.5 | | | | 9.5 | 90.0 | | | | 10.0 |
| Lightest | 82.0 | | | | 18.0 | 62.5 | | | | 37.5 |
| Averages | 86.1 | 4.7 | 2.4 | 6.8 | 13.9 | 76.1 | 8.4 | 4.0 | 11.5 | 23.9 |
| Series *C* (pool): | | | | | | | | | | |
| Extremes: | | | | | | | | | | |
| Darkest | 93.0 | | | | 7.0 | 90.0 | | | | 10.0 |
| Lightest | 77.5 | | | | 22.5 | 61.0 | | | | 39.0 |
| Averages | 86.6 | 4.5 | 3.1 | 5.8 | 13.4 | 78.3 | 7.7 | 4.2 | 9.8 | 21.7 |

It will be noted that the series reared in laboratory light (Series *B*) and the one developing under natural conditions in the outdoor pool (Series *C*) agree very closely in the amount of pigment development, the average percentages of black in the body color determinations being 86.1 and 86.6, and for the head color 76.1 and 78.3 respectively, while the extremes for the two series differ but slightly. However, the most significant fact is that these series differ so sharply from Series *A* reared in the dark and having an average body color of only 49.7 per cent. black and an average head color of 38 black. On the average those reared in darkness have about four times as much non-black in the body color as those reared in light, while the darkest individual of the cave series, really aberrant for that series because it is so dark with 70.5 per cent. black in the body color

and 51 per cent. in the head color, has decidedly less pigment than the lightest individual of either Series *B* or Series *C*, with 77.5 per cent. black in the body color and 61 black in the head color.

The percentage differences in color between the series reared in darkness and the two series reared in light do not adequately represent the color differences as perceived by the eye. The average person probably would not hesitate to call the lighter individuals of Series *A* "white," and on the other hand would probably class the various individuals of Series *B* and *C* as "dark gray" or "coal black."

There appear to be no reasons for thinking that the marked differences in pigment development were due to differences in nutrition or differences in temperature. Series *B* so closely resembled Series *C* in amount of pigment development that it is evident the differences in temperature and food did not greatly influence their pigmentation, yet Series *B* was reared in a west room subject to great fluctuations in temperature because of the extreme exposure to the summer sun during the afternoon, and the temperature of this series on the average was probably higher than in the outdoor pool in which Series *C* developed, while the food was exclusively daphnids, copepods and bits of beef. On the other hand Series *A* was maintained at a quite uniform temperature consistently lower than either of the other series. Fischel ('96) and Flemming ('97) found that with certain salamander larvæ (the former at least used larvæ of *Salamandra maculata*) temperature differences influenced the amount of pigment development, the individuals reared at from 4° to 7° C. being much darker than individuals reared at from 15° to 20° C., indicating that for *Salamandra maculata* the lower temperature favors greater pigment development. Inasmuch as my lightest series, Series *A*, was reared at the lowest temperature of any and yet was markedly lighter than the others, and that Series *B* and *C* did not differ widely in amount of pigment development although reared under somewhat different temperature conditions renders it improbable that temperature influences produced the differences in pigmentation observed.

Series *A* and *B* were fed in every way alike and so far as could be judged took about the same quantities of food. While as a whole Series *A* developed less rapidly than Series *B*, part of Series *A* developed more quickly than some of Series *B* yet each individual possessed an amount of pigment similar to the others of its series. Hence the evidence strongly points to the con-

clusion that the differences in amount of pigmentation were not due to differences in temperature, food or rate of development but solely or in much the greater part to the absence or presence of light.

The difference in pigmentation between Series *A* on the one hand and Series *B* and *C* on the other is fully as great as the difference in pigmentation between certain species that live habitually in caves and others which do not. To this point the case looks most significant. With the approach of transformation, however, the amount of pigment rapidly increases, particularly on the lighter regions of the larvæ, and this increase is more pronounced with those reared in darkness than with the others. Nevertheless there still remains a marked difference in pigmentation between the transformed individuals of Series *A* reared under cave conditions and Series *B* reared in the light.

Color records of a few recently transformed salamanders were taken before the spots so characteristic of the adult were definitely formed. An attempt was made to get careful records of the general blended color effect independent of the mottling which is quite pronounced at this stage, during which the pigment is being segregated to form the definite color pattern of the adult. The average body color of the transformed salamanders of Series *A* was 70.2 per cent. black and 29.8 per cent. non-black, and the average head color 68.2 black and 31.8 non-black. These averages for Series *B* are: Body color, 89.7 black and 10.3 non-black; head color, 87.7 black and 12.3 non-black. No transformed individuals of Series *C* were obtained. Unfortunately records of transformed individuals of Series *A* and *B* were made of only 2 and 5 individuals, so these are scarcely more than sample records, but they are probably fairly representative of their respective series, and they clearly indicate that after, as well as previous to, transformation a distinct difference in pigmentation persists between the salamanders reared and allowed to transform in the cave and those developing and transforming in the light.

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